Impacts of disturbance on the dynamics of marine benthic communities

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For my Dad, for all of his time spent debating the point and for being a fighter.

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Abstract

Disturbances are one of the most important factors in maintaining the co-existence of species, and their frequency, intensity and timing are all thought to be increasing as a direct consequence of anthropogenic global change. Therefore many species may not be able to adapt and may subsequently be lost from an ecosystem. The aim of this thesis is to focus on the local scale processes in benthic subtidal habitats that are thought to drive the co-existence of species within communities. The primary goal was to investigate disturbances and their impacts upon temperate marine benthic communities, and secondary aims explored the interactions between disturbances, productivity and habitat complexity. In order to test the intermediate disturbance hypothesis and a model of disturbance-productivity interactions, communities of two different successional stages were manipulated with a range of disturbance frequencies and varying levels of nutrient availability. The effect of temporal variation around the disturbance regime which caused the greatest effect, as well as the sequence of these disturbances, was then investigated. Finally the role of natural surface heterogeneities in creating refuges in the face of a suite of different disturbances was investigated, and used to discover the value of increasing habitat complexity in maintaining or promoting diversity. Results from all experiments have shown that disturbances are important structuring forces for benthic marine communities. Disturbance-productivity interactions do not support the intermediate disturbance hypothesis or the disturbance-productivity model and the temporal variability of disturbance regimes appears to be an unimportant factor in the structuring of these temperate communities, whereas increased habitat complexity provides important refuges in the presence of abiotic disturbances.

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Chapter One: Introduction

1.1 - The Importance of biodiversity: mechanisms of co-existence, economics and conservation

Biodiversity is the number and variety of living organisms, as well as the variability among these organisms, including the variability within and between species and within and between ecosystems, it includes the entire range of species found on Earth (Wilson 1988, Primack 2002). More specifically species diversity is a function of the number of species present (their richness), and the evenness with which the individuals are distributed among these species (Hulbert 1971). Species diversity can be calculated in a number of indices but for the sake of clarity the Shannon Index (H') for diversity was used throughout this thesis (Magurran 1988) as it is a common measure for species diversity. The Shannon index is calculated from the species richness (a count of the number of species present) and evenness (using Pilou's evenness), the calculation for which are shown below:

$$\text{Shannon Index:} \quad H' = -\sum_{i=1}^{s} p_i \ln p_i$$

$$\text{Pielou's Evenness:} \quad E = \frac{H'}{H'_{max}}$$

Where n_i is the abundance of each species, s is the number of species (species richness), N is the total abundance $\sum_{i=1}^{s} n_i$, p_i the relative abundance of each species, calculated as the proportion of abundance of a given species to the total abundance of individuals in the community $\frac{n_i}{N}$. H' is the number derived from the Shannon diversity index and H' max is the maximum value of H' (Magurran 1988).

Disturbances are important forces in the structuring and development of many types of ecosystems (Ayling 1981, Sousa 1984). They act as a mechanism to reset succession and allow the co-existence of species, whilst releasing essential limiting resources for utilisation by these plants and animals (Connell 1978). A disturbance can be defined as "a temporally discrete event which abruptly kills or displaces individuals, or that directly result in the loss of biomass from a system" (see section 1.6.1: Grime 1977). According to this definition they are dynamic and natural processes affecting community structure at different spatial and temporal scales (Pickett & McDonnell 1989).

Numerous concepts have been formulated about the possible outcomes of a disturbance on a community, the most famous and widely applied of which is the 'Intermediate disturbance hypothesis', conceived for the extremely diverse tropical rainforests and coral reefs (Connell 1978). However, although based on sound theory, this hypothesis has been internationally applied as a management tool in a variety of different ecosystems (Roberts & Gilliam 1995, Odion & Sarr 2007), despite the fact that the majority of empirical studies do not support the model (Mackey & Currie 2000). The effects of disturbances on community diversity remain elusive and their interactions with other structuring forces are poorly understood. This thesis aims to investigate the effects of abiotic disturbances in benthic marine ecosystems, and attempts to examine the interactions between disturbances, productivity, temporal variation and spatial heterogeneity.

Species diversity is essential to the functioning of the Earth turning geochemical processes into biogeochemical processes (Naeem et al. 1994). Biological systems therefore provide a number of life support services such as, fresh air, clean water and food whilst also cycling compounds such as carbon dioxide and nitrogen, all of which maintain an atmosphere conducive to life and are essential to our continued survival (Worm et al. 2002, Naeem 2006). But species are being lost at an accelerating rate due primarily to anthropogenic impacts (Gray 1997, Sala & Knowlten 2006). Disturbances in ecosystems have long been recognised as a major force which facilitates the co-existence of species, but as anthropogenic impacts become greater, disturbance regimes (from influxes of predation to hurricanes) are shifting, potentially altering them from mechanisms that allow the co-existence of species to mechanisms that become so frequent and intense that they begin to exclude species from ecosystems (Michener et al. 1997).

1.2 - Species Diversity

There are more species on Earth in the present geological period than in any other, yet most ecological systems are experiencing a loss in biodiversity greater now than in any other period. This reduction in species diversity seems destined to be the most extreme in the past 65 million years, more so than the natural catastrophes at the end of the Palaeozoic and Mesozoic eras (Kim & Byrne 2006). Extinction is a natural process (Chapin et al. 2000) but the rate of the modern episode of extinction is exceeding anything in the geological past,

primarily because for the first time plant diversity is also sharply declining (Table 1.1: Knoll 1984, Wilson 1988).

The five major extinctions throughout geological time have always been caused by catastrophic natural disasters. However, the cause of the current loss in biodiversity has changed and is no longer attributable to external forces. For the first time the current extinction is due principally to exploding human populations (Table 1.1) which are degrading the environment at an accelerating rate, especially in the tropics, resulting in five principal threats: (i) the destruction, fragmentation and loss of habitats; (ii) the introduction of exotic species and diseases; (iii) over-exploitation; (iv) pollution and; (v) climate change (Soule 1991, Suchanek 1994, Gray 1997, Butchart et al. 2006, Sala & Knowlten 2006).

Table 1.1 – Summary of major extinctions occurring over geological history, including suspected causes and taxonomic groups lost (data summarised from IUCN 1995-2007, Fossil 2001-2007, Bristol University 2007).

Extinction	When	Caused by;	% Families lost	Most Affected
Ordovician	440 mya	Drop/rise in sea level Glaciers forming and melting	25 %	Trilobites suffered but survived >50 % bryozoans and brachiopod species extinct
Devonian	370 mya	Unknown	19 %	Marine environment lost fish and reef building invertebrates
Permian	250 mya	Volcanic eruption – Siberian traps	54 %	Most catastrophic loss of life to date, 95 % marine species and 70 % land species lost Trilobites extinct
Triassic	210 mya	Changes in sea level Volcanic eruptions Meteorite impact	23 %	Claimed mammal like reptiles and invertebrates Ammonites suffered
Cretaceous	65 mya	Meteorite impact	17 %	Dinosaurs extinct Ammonites, fish, clams, snails, sponges and sea urchins suffered
Quaternary	Present day	Anthropogenic activities	?	Hardest hit so far; beetles amphibians, birds, large mammals

1.2.1 - Destruction, fragmentation and loss of habitats

Habitats across the world are being lost at an alarming rate. Across the globe there are 25 hotspots of biodiversity which are home to a third of terrestrial vertebrates and nearly half of the world's vascular plants. Historically these

hotspots covered 12 % of the lands surface but today their intact habitat makes up only 1.4 % (Myers et al. 2000). This has implications for the species living within these habitats which are threatened with extinction, more so because they are endemic to these areas of unique habitat (Brooks et al. 2002). However, these trends are not just confined to the hotspots of diversity; they are occurring all over the world, in all types of habitat due to the effects of deforestation, changes in land usage and development (Gray 1997). This loss in habitat eventually produces an area that is unsuitable for supporting populations of target species or maintaining community diversity (Acosta 1999).

The commonly occurring loss of habitat across the world is not however a continuous one, it is often confounded by extensive habitat fragmentation, most notably in forest and marine habitats, creating patchy environments (Gray 1997, Fischer & Lindenmayer 2007). The spatial proximity of one habitat to another can strongly influence population and community dynamics and ultimately the function of that particular ecosystem (Micheli & Peterson 1999).

Experiments have shown that fragmentation of habitats creates a series of patches or 'habitat islands' surrounded by a series of edges. The fragment edges and spaces in between habitats have a different microclimate (and therefore environmental conditions) than the inside of the remaining patch (Kupfer et al. 2006, Fischer & Lindenmayer 2007). The size of the patch is strongly correlated with the edge in determining how far into the patch this new microclimate can penetrate (Moen & Jonsson 2002). Studies on forest patches have revealed that although the response to edge effects is strongly species dependant, in the

presence of edges the fragments were shifting to a species poor seedling community, therefore resulting in a loss of species, and potentially functional, diversity (Moen & Jonsson 2002).

Habitat fragments not only prevent the survival of some species, for the species that do survive, the populations often find themselves isolated, unable to cross the 'void' that has been created. Once a population is isolated in this way its survival comes into question (Wilson 1988). This population can no longer migrate to exploit resources, such as food, and they cannot interbreed with other populations resulting in a loss of genetic diversity. A possible solution (with evidence of some successes in the marine environment, Acosta 1999, Kirchner et al. 2003) to this has been the introduction of habitat corridors, where all the patches are linked together with a series of passageways of intact habitat (Acosta 1999, Micheli & Peterson 1999, Kirchner et al. 2003). However, this still represents some difficulties for species whose differing life stages require different habitats (Acosta 1999); it isn't possible to tell whether they will conveniently use the corridors that are laid out for them, nor whether the corridors are large enough to negate their own edge effects. In theory the use of such corridors presents a successful solution to a growing problem but there is little strong empirical support to this theory with some studies showing that they may even have deleterious effects on species diversity (Davies & Pullin 2007).

1.2.2 - Introduction of exotics

Biological invasions of exotic or alien species are recognized world wide as a very serious ecological problem and a significant component of anthropogenic global change (Dukes & Mooney 1999, Piazzi & Cinelli 2003). Although these introductions have been occurring for thousands of years they have dramatically increased over the last few decades (Piazzi & Cinelli 2003) due to technological advances (Everett 2000). Second to habitat loss, destruction and fragmentation, the introduction of exotic species is thought to be one of the most important causes for the decline in native species across the world (Everett 2000, Altman & Whitlatch 2007). The increased rate of invasion by these species has affected terrestrial, aquatic and marine habitats, with the latter being one of the most invaded systems due to urbanization of coastal habitats, exploitation of fisheries, international shipping and aquaculture (Piazzi et al. 2001, Piazzi & Cinelli 2003, Altman & Whitlatch 2007).

The introduction of biologically invasive species has resulted in many ecological problems including:

- The reduction of native biodiversity by invasive species that are superior competitors/colonisers of space. Resulting in a possible homogenization of the world's biota (McKinney & Lockwood 1999, Stachowicz et al. 2002, Facon et al. 2006, Altman & Whitlatch 2007).
- Replacement of the dominant species and shifts in communities and their trophic levels, ultimately impacting on ecosystem function (Walker

& Kendrick 1998, Casas et al. 2004, Facon et al. 2006, Altman & Whitlatch 2007).

- Public health risk, with accelerated growth of diseases that are transported by insects, such as malaria, as well as introduced diseases in native species populations (Dukes & Mooney 1999, Facon et al. 2006)
- Damage to commercially important species, fisheries and aquaculture (Casas et al. 2004, Facon et al. 2006, Altman & Whitlatch 2007)

There are two different types of biological invasions; "range expansions" which include dispersal by natural mechanisms, but will be facilitated by global climate change, where habitats that were previously unsuitable to the invading species become modified to fit their niche requirements (Carlton 1989, Dukes & Mooney 1999, Facon et al. 2006), and "introductions" which are classed as dispersal by human activity and often occur across natural barriers and vast distances (Carlton 1989, Facon et al. 2006). The success of an invasive species is also linked to disturbances; with frequent and intense disturbance events likely to become 'the norm' (see section 1.2.5) the success of invasive species is likely to increase as free space for their colonization is opened up (Stachowicz et al. 1999, Kennedy et al. 2002, Altman & Whitlatch 2007). Experimental studies have also shown that the more diverse an ecosystem is the more resilient to invasions it becomes. However, as already mentioned we are experiencing the greatest loss in biodiversity to date (Chapin et al. 2000), thus entering into a positive feedback cycle where we are losing biodiversity. This allows the invasion of more exotic species to occur, and subsequently more diversity is lost (Stachowicz et al. 1999).

1.2.3 - Over-exploitation

Although the need to maintain biological diversity has received increasing attention from scientists and politicians over the last few decades, little effort has been invested in conserving the biological diversity of the oceans and seas. Marine systems not only provide food but they also remove a large portion of CO_2 from the atmosphere (Upton 1992). The over-exploitation of marine resources has now become a major threat to its biodiversity (de Boer & Prins 2002), and reductions in important plant and animal species are placing a great stress on the viability of many ecosystems (Islam & Haque 2004). But this exploitation by humans depends largely on the particular species being targeted and the size of the catch (de Boer & Prins 2002). The most obvious example to explain the over-exploitation of marine resources is of course the present status of the world's fisheries. A global crisis in marine fisheries was viewed by many with scepticism as little as ten years ago. Despite this, there has been a decline in global fisheries catches since the late 1980s, but instead of taking note, fishing effort and catching power has continued to increase (Morato et al. 2006).

Fisheries exploitation has therefore spread from coastal areas, to the open ocean and with the present decline of shallow coastal water resources and increasing demand, new technologies are allowing the fisheries to expand into deeper waters: the final refuge for many pelagic species. Deep water fish have a high longevity, slow growth, late maturity and a low fecundity, making them more vulnerable to exploitation than most species and possibly allowing them to be rapidly depleted (Morato et al. 2006). This is seriously altering species

compositions and causing a loss of biodiversity from ecosystems (Ukwe et al. 2006). Moreover, it is not just fisheries that are being over-exploited; the exploitation of benthic intertidal invertebrates is so extensive that many community structures are being altered (de Boer & Prins 2002). Trochus shells, sea cucumbers and turtles are just some of the species that are highly desired in the tropics and Asia (Richards et al. 1994), and more recently with the successful discovery and extraction of novel medical compounds from areas such as coral reefs, exploitation is thought to increase (Hodgson 1999).

1.2.4 - Pollution

Marine pollution is the anthropogenic introduction, directly or indirectly, of substances or energy into the marine environment resulting in deleterious effects such as hazards to human health, hindrance of marine activities (including fishing), impairment of the quality and use of seawater, and a reduction in amenities (Clark 2001). It is the most subtle and universal form of environmental degradation and is commonly caused by pesticides, sewage, fertilizers, industrial chemicals and wastes, emissions from factories and automobiles, sediment deposits and oils spills (Primack 2002, Guidetti et al. 2003). As a result of this many plant and animal species and the ecosystems in which they live are being degraded (Spellerberg 1992).

One of the most documented, serious and increasingly common forms of marine pollution is sewage (Gappa et al. 1990, Smith et al. 1999, Espinosa et al. 2007). It is often discharged via outfalls and affects can be seen locally as well as many

kilometres away (Smith et al. 1999) and it produces significant deleterious effects on marine biota resulting in changes in cytology and physiology of individuals, which are ultimately passed along the food chain to produce alterations at the community level (Smith et al. 1999, Espinosa et al. 2007). This usually results in a reduction of diversity of intertidal and shallow subtidal assemblages, and changing community compositions to become dominated by a few species of macroalgae (Hardin 1960, Smith et al. 1999, Bishop et al. 2002).

1.2.5 - Climate Change

The Earth's climate is changing at an accelerated rate (Delbaere 2005, Harley et al. 2006). Over the past 100 years the Earth's climate has risen by approximately 0.7 ^{0}C with two significant periods of warming between 1910-1945 and 1976 onwards (this rate doubled the previous, making it the greatest period of warming for 1000 years) (Walther et al. 2002, Delbaere 2005). The International Panel on Climate Change (IPCC) have attributed these increases in temperature, predominantly to human activities, namely the emission of greenhouse gases (IPCC 2001, Delbaere 2005, Harrison et al. 2006) and they predict that temperatures will rise between 1.4 – 5.8 ^{0}C by 2100 (Smith & Buddermeier 1992, Michener et al. 1997, Harrison et al. 2006). A major effect of these increased temperatures has occurred on diurnal temperature ranges which are decreasing. Minimum temperatures are increasing twice as fast as maximum temperatures leading to longer freeze free periods at higher latitudes and a 10 % decrease in snow cover and ice extent since the 1960s.

But temperature is not the only environmental parameter expected to be affected. Precipitation patterns, oceanic and atmospheric circulation, the rate of rising sea levels, the frequency, intensity, timing and geographical distribution of hurricanes and tropical storms, as well as the duration of the hurricane season are all predicted to change (Michener et al. 1997). However, the changes that have been predicted are not something that is going to happen in the future. Their effects are already being seen by a number of field biologists (in both physical and biological systems) who are working to provide the evidence with which to convince the world that these changes are upon us (Penuelas & Iolanda 2001, Walther et al. 2002, Parmesan & Yohe 2003, Harrison et al. 2006).

The simplest biological process that can be used to track climatic change is the Phenology, or timing of seasonal activities, of both plants and animals (Penuelas & Iolanda 2001, Walther et al. 2002, Parmesan & Yohe 2003, Delbaere 2005) and there are many examples in the literature such as, earlier shooting and flowering of plants and the earlier appearance of butterflies (Walther et al. 2002). But this is not the only biological process where the changes can already be seen. There have been observations of shifting distribution ranges of species habitats, which is leading to the 'summit trap phenomenon'. As southern species move north to stay within their optimum temperature ranges, the northern species or those at the top of mountain ranges become 'squeezed', they have nowhere to go to stay within their desired habitats. They become locally extinct, but because many live in unique habitats and are endemic to these areas, they are faced with global extinction (Delbaere 2005). Even if the Northern species can adapt to the changing environment they then face extreme competition with

the invading Southern species. Effects on plant physiology and changing community structures and species interactions have also been reported (Delbaere 2005).

1.3 - Importance of Ecosystems and biodiversity

The five principal threats that have been listed above have all been described independently of one another, and as severe as their consequences appear to be this does not tell the whole story. These threats all interact with one another facilitating the loss of biodiversity to a greater extent than if we were just dealing with one at a time (Fig. 1.1).

All of the changes that are being observed in biological systems may consequently lead to the irreversible extinction of many species, as well as a loss of habitats, raising the issue as to whether the function of ecosystems will be impaired by this loss (Soule 1991, Naeem et al. 1994, Pimm et al. 1995, Naeem & Li 1997).

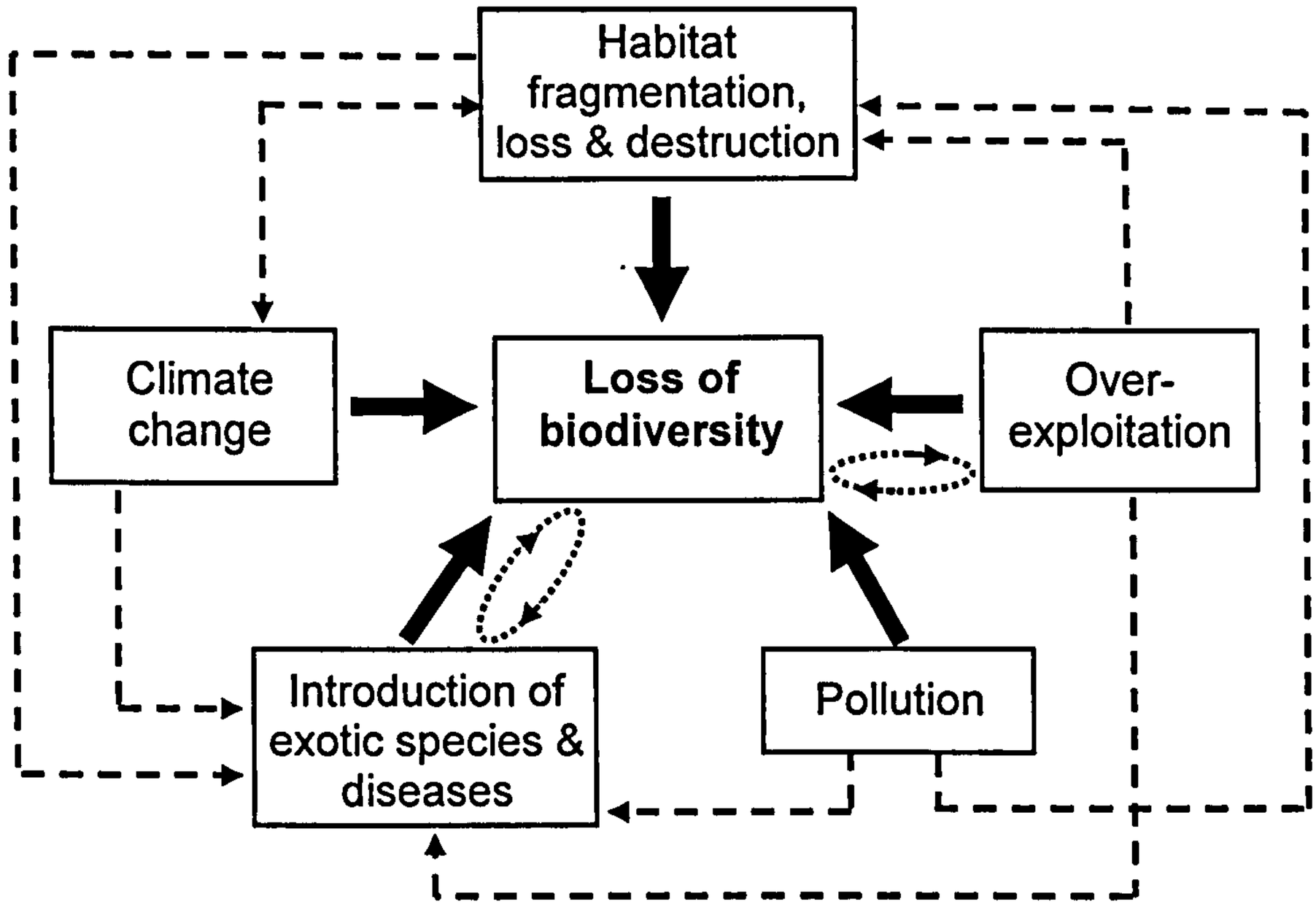


Figure 1.1 – The interactions between the principal threats to the loss of biodiversity: With every indirect or facilitating component that is added to the model, the relative contributions of each threat to the loss of biodiversity becomes greater, creating in some cases positive feedback cycles, inevitably speeding up species extinctions where: ➡ *represent direct impacts,* ⇢ *represent indirect or facilitating impacts, and* ⟲ *represent positive feedback cycles.*

Ecosystems drive the Earth's biogeochemical processes (Naeem et al. 1994) and it is now generally accepted that the functioning and sustainability of these ecosystems depends on their biological diversity (McGrady-Steed et al. 1997, Naeem & Li 1997, Kim & Byrne 2006). Elton (1958) proposed that the more diverse an ecosystem the more stable and therefore predictable it becomes (Tilman 1996), and an extreme loss in biodiversity is thought to cause a functional deterioration in all ecosystems. Since all levels of biodiversity

(genetic, species and ecosystem) are essential for the continued survival of natural communities and therefore humanity (Primack 2002), knowledge of ecosystem predictability is essential to facilitate ecosystem management. It provides a convincing argument for conserving species richness in relatively intact ecosystems and restoring diversity in degraded systems (McGrady-Steed et al. 1997).

The fundamental importance of the role of biodiversity in ecosystems has been described by Naeem (2006) and Worm et al (2002). The Earth's biota regulate the biogeochemical processes, which annually move gigatons (gt) of material (such as carbon, nitrogen and phosphorus) among the hydro-, litho- and atmosphere producing an environment conducive to life (Naeem 2006). In the absence of the biota the processes become purely geochemical. The Earth's biota can be split into two components, its biomass and its biodiversity (structure of biomass), both of which are inextricably linked and together influence ecosystem functioning. The amount of, and fluctuations in, atmospheric CO_2 over the past 370 million years has been driven almost entirely by the biosphere. This implies that human dominance over the biosphere leaves the carbon cycle (and every other biogeochemical process for that matter) increasingly in the hands of humans, many of whom are not even aware that it exists (Naeem 2006). An example of ecosystem function is the carbon cycle. Reductions in the biosphere through losses of biodiversity consequently result in a percentage of carbon not being cycled. This is readily transferable to other ecosystem functions (Worm et al. 2000, Naeem 2006). This will directly impact

the supporting services that we take for granted and are essential to the continued survival of mankind (Balvanera et al. 2006, Costanza et al. 2007).

Diversity has also been linked to the level of productivity within a system. When consumers are present the level of productivity needed to maintain peak diversity increases. But humans are altering the levels of nitrogen and phosphorus in the environment (Worm et al. 2002), which results in an increase in the levels of productivity in all systems. Added to this we are altering consumer pressure through overexploitation, habitat destruction and fragmentation. All of which is compromising the ability of ecosystems to retain the excess nitrogen put upon them by pollution from human activities (Chapin et al. 2000, Worm et al. 2002).

Another reason for conserving species diversity is the proposed gains for humanity. Every time we lose a species we lose a potential option for the future. Approximately 1.75 million species have been described to date, but this is only a fraction of the estimated 5 - 30 million species that actually exist (Wilson 1988, Kim & Byrne 2006). Imagine the possibilities for future resources, such as drugs and energy, contained within the species that we have yet to discover, but despite this we are allowing our activities to eliminate these species along with potential solutions to our future survival (Carpenter et al. 2006).

1.4 - Economics and Conservation

The vast majority of mankind is buffered from nature by culture and technology, leading to an increased separation between humans and the natural world (Carpenter et al. 2006) and a decreased value and understanding of biodiversity. Ecosystems provide a number of "services" which contribute to the well being of the Earth and therefore directly to the well being of mankind (Wilson 1988, Costanza et al. 1997, Edwards & Abivardi 1998). Unfortunately due to this separation from nature the ecosystem services, which are essential to the functioning of our planet, are being depleted, with a recent review showing approximately two thirds in decline (Alcamo et al. 2005). Ecosystem services are given too little weight in policy decisions, because they are not fully captured in commercial markets, or adequately quantified in terms comparable with economic markets. Until a realistic price is put on the services that ecosystems provide, and therefore the ecosystems themselves, it will never be possible to conserve them because politically they are seen as having no real value in economic terms (Costanza et al. 1997).

Costanza et al (1997) recently estimated the natural processes which provide the majority of ecosystem to be worth $67 billion per year when they were previously thought to have no economic significance. Nevertheless as ecosystems become inevitably more stressed, through losses in biodiversity, the services they provide will become scarcer and harder to artificially create, and so the economic value of ecosystem services will continue to dramatically increase (we will never be able to recreate these services as well as they were

created in the first place) (Costanza et al. 1997, Edwards & Abivardi 1998, Antoci et al. 2005, Straton 2006). Ecosystem services can be split into four different categories (Fig. 1.2) but the priorities of maintaining each of these categories may lead to an irreversible loss in the fundamental services which underpin all others (Rodriguez et al. 2006, Straton 2006). A principal difficulty in managing ecosystem services is that they are all interconnected with one another, by exploiting one service we will inadvertently affect another. A knowledge and awareness of the services is essential for making decisions on how to manage them (Rodriguez et al. 2006).

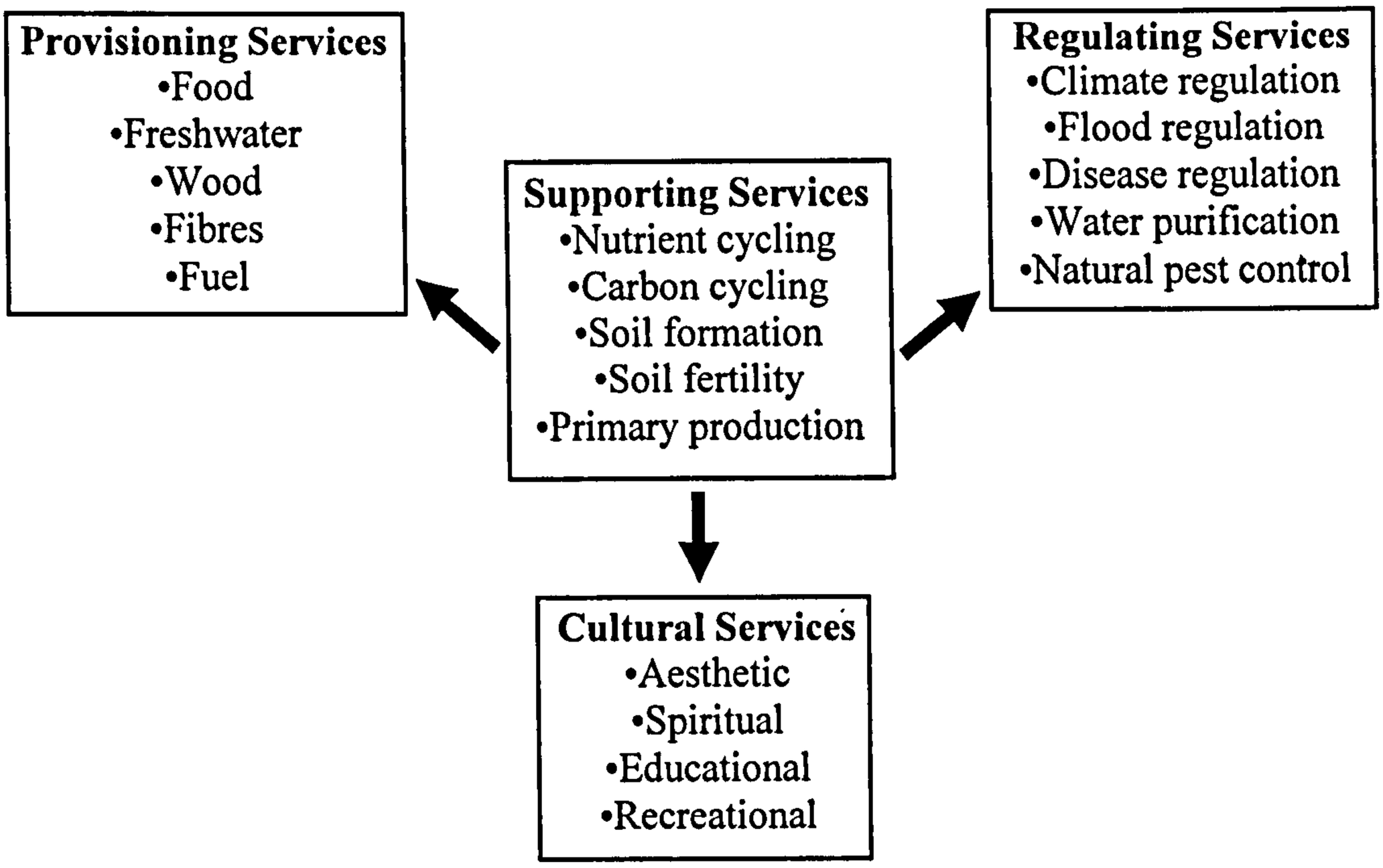


Figure 1.2 – Ecosystem Services: biodiversity underlies all ecosystem services. They include provisioning, regulating and cultural services, and the supporting services are those needed to maintain all of the others (adjusted from Rodriguez et al. 2006).

This inevitably leads to a trade off between certain services, and the majority of these will derive from management decisions made by humans (Rodriguez et al. 2006). In trade off decisions management plans prefer to optimise provisioning services, followed by cultural and then finally regulating services which therefore undermines the supporting services and slowly changes the components which provide them (Rodriguez et al. 2006). Yet the recognition of the need to put a price on ecosystem functioning is an important step forward in conservation and becomes an effective tool for conservationists. Biodiversity can therefore be measured as an essential yet diminishing resource (Straton 2006, Winkler 2006a, b)

However, economics will always underestimate the true value of biodiversity because there is a lack of knowledge about the role of a particular habitat/species in providing life support functions. It is also important to note that we have no idea as to the importance of the existence of a particular species to the stability of the ecosystem under unknown conditions in the future (Carpenter et al. 2006). By conserving as many species and functional groups within intact ecosystems as possible, we provide an 'insurance' against future environmental change, it is not guaranteed and it cannot substitute for not reducing other kinds of anthropogenic stresses to ecosystems, but it does provide a chance for the continued survival of the services that we take for granted (Bengtsson et al. 2000, Chapin et al. 2000, Carpenter et al. 2006).

Nevertheless, changes in policy making is likely to increase the recognition that biodiversity is a 'public good', billions of dollars have been invested to reduce

the loss of biodiversity in developing nations. Conservationists are trying to produce incentives to conserve ecosystems and species, while governments are working together to provide an international solution to the growing crisis (Ferraro & Kiss 2002).

1.5 - Mechanisms Creating Species Diversity

The mechanisms creating observed patterns of biodiversity have long been of interest to community ecologists (Huston 1994, Rosenzweig 1995, Mackey & Currie 2001) and it is essential that as ecologists we aim to understand what mechanisms create and maintain the co-existence of species in order that we can begin to conserve intact communities and attempt to restore degraded ones for the reasons outlined earlier in this chapter.

Over the past 50 years many hypotheses have been developed to try and explain patterns of species diversity, and they fall into two main concepts: equilibrium and non-equilibrium models. Equilibrium models state that once a community recovers from a severe perturbation, diversity is maintained near an equilibrium state by competitive exclusion where the competitively dominant species persists and high diversity is maintained through exploitation of different resources (Hardin 1960). Under these circumstances the high diversity that was observed was thought to be maintained by processes such as niche partitioning (Connell 1978). Non-equilibrium models suggest that communities seldom or never reach an equilibrium state and that diversity is a consequence of continually changing conditions maintained by a number of factors (Hardin

1960, Connell 1978, Huston 1979, McAuliffe 1984, Collins & Glenn 1997, Floder & Sommer 1999).

Historically, equilibrium models dominated ecological thinking, but patterns of diversity in the field were not compatible with these models (Hutchinson 1961, Connell 1978, Pickett & McDonnell 1989, Collins & Glenn 1997). More recently with the recognition that natural communities are variable and exist in a continually changing environment, ecological sentiment has shifted in favour of non-equilibrium explanations of species co-existence and community structure (Collins & Glenn 1997). The most common of these non-equilibrium explanations is the intermediate disturbance hypothesis (IDH: Fig. 1.3), which states that maximum diversity will be achieved at intermediate disturbance frequencies and intensities due to a trade off between competitive and colonising abilities (Connell 1978). Other explanations include the dynamic equilibrium model (Fig. 1.4) which is an extension from the IDH stating that the intermediate frequency will shift depending on the productivity of a system (Huston 1979).

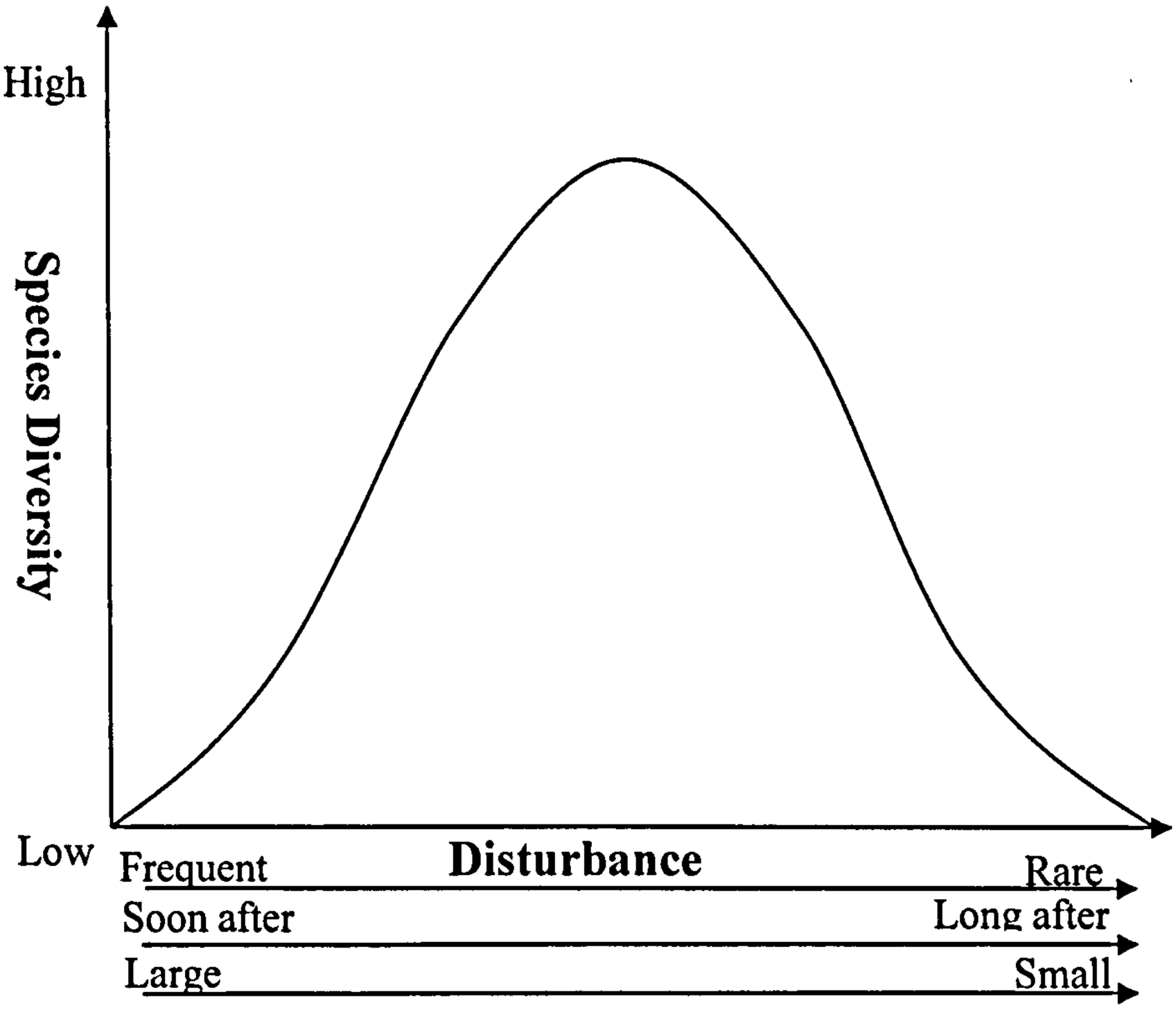


Figure 1.3 – The intermediate disturbance hypothesis: Maximum species diversity occurs at intermediate frequencies and intensities, as well as intermediate time since the last disturbance, since superior competitors and colonisers can coexist (copied from Connell 1978).

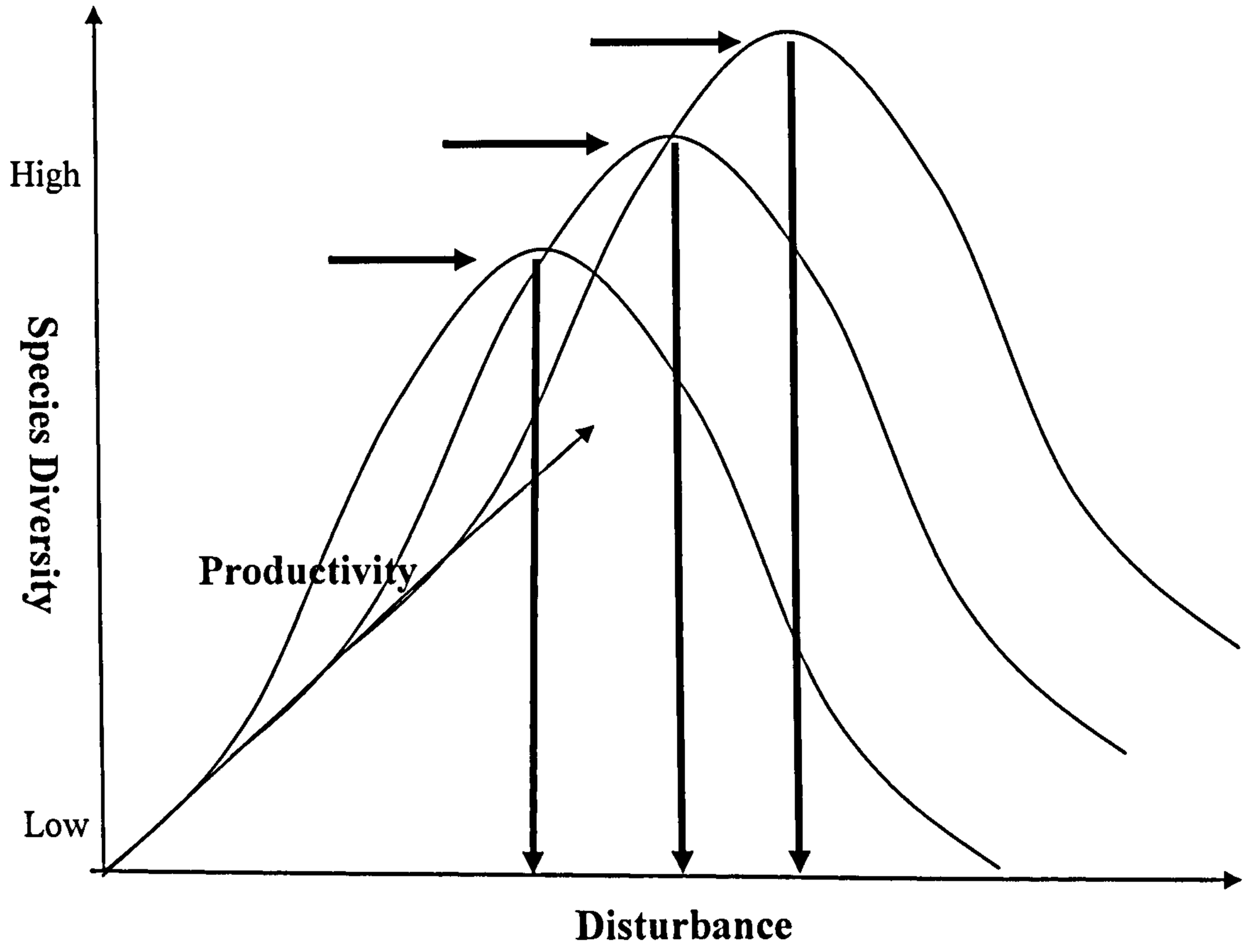


Figure 1.4 – The dynamic equilibrium model: first described by Huston (1979) and later elaborated by Kondoh (2001). The point, at which maximum species diversity is achieved as hypothesised by the IDH, will shift depending on the productivity of that system. It can be seen that as productivity increases the disturbance frequency/intensity/time is also increasing (adjusted from Kondoh 2001).

Several theories (MacArthur & Wilson 1967, Fukami 2004, He et al. 2005, Fox 2006) and studies (Hillebrand & Blenckner 2002, Kreft & Jetz 2007) have sought to explain the mechanisms that allow the co-existence of a large number of species (Smith & Witman 1999), and the realization of the importance of scale has stimulated new hypotheses about how species assemblages are maintained.

Throughout the biosphere species diversity is distributed heterogeneously varying both spatially and temporally; some areas team with biological diversity (e.g. coral reefs) whilst others are seemingly devoid of life (e.g. deserts) (Gaston 2000). Understanding the forces that shape these spatio-temporal patterns in species diversity remains a major issue confronting ecologists (Witman et al. 2004), and there is a general lack of consensus about the mechanisms leading to many of the observed gradients (Hillebrand 2004). Despite this there is a general agreement that no single mechanism explains a given pattern, and that multiple processes interact to influence patterns of species diversity at different scales (Gaston 2000, Fukami 2004).

One general and increasingly recognised pattern in ecology is the frequently observed linear relationship between the species richness of local communities and the richness of the regional pool (Fox 2006). Experiments conducted at local scales demonstrate that the local processes such as biological interactions, productivity, habitat complexity, disturbance, environmental stress and parasitism, interact to produce variability in local species richness (Hillebrand & Blenckner 2002, Witman et al. 2004, He et al. 2005, Russell et al. 2006). But

these local processes must also be affected by regional scale processes (long distance immigration, speciation and evolutionary history, climate and climate variability: Pianka 1966, He et al. 2005) because local communities are integral components of larger bio-geographic regions (Witman et al. 2004). These regional scale processes provide a source of species to colonise and enrich local assemblages (He et al. 2005, Russell et al. 2006).

Many other patterns of spatial variability in biodiversity have been explored. The theory of island biogeography discusses species area relationships, stating that with an increase in the area of a given space, species diversity will generally increase (MacArthur & Wilson 1967). The temperate-tropical gradient outlines the very noticeable pattern of greater species richness in tropical areas with diversity decreasing at higher latitudes. This is thought to occur due to lower productivity at high latitudes and low climate variability at low latitudes, effectively producing a more stable environment reducing the need to have high environmental tolerances (Gaston 2000, Mittelbach et al. 2007). Other hypotheses have sought to explain patterns at depth (Brandt et al. 2007, Coleman et al. 2007), altitude (Grytenes et al. 2006) and productivity (Connell & Orias 1964). Despite the vast array of studies that are carried out into the explanation of species diversity, the majority of studies are carried out in terrestrial and freshwater systems and relatively little is known about diversity patterns in the marine realm. This is due primarily to its vastness and inaccessibility, and patterns within this environment appear to be more complex than those already described for terrestrial systems (Hillebrand 2004).

1.6 - Rocky Shore and Patch dynamics

Sessile benthic communities on temperate rocky shores offer one of the very few biological systems that can be manipulated so that there are comparable altered and unaltered states (Dayton 1971). The biota found in these ecosystems, both intertidally and subtidally, are diverse, abundant and sedentary (Smith & Witman 1999). They have the logistical advantage of being readily accessible (unlike most marine environments) where most species are limited to rocky substrata, with space as a limiting resource (Matthaei et al. 2003), and they have wide overlapping geographical ranges (Dayton 1971). Community assemblages on rocky shores have short generation times and they recruit on large scales (Bampfylde et al. 2005), making the composition of these sessile communities particularly useful as a baseline for ecological monitoring because such organisms are unable to avoid disturbances. Therefore the composition of the community reflects their common history (Espinosa et al. 2007), and they are characterised by continuous physical and biological disturbances, an abundance of free space and a large number of species which utilize the same limiting resource (Dayton 1971).

Ecosystems are therefore comprised of very dynamic communities that are continually changing and are comprised of a mosaic of patches of different successional stages due to the common nature of disturbances in this environment (see section 1.6.1). Disturbances, and their size, frequency and intensity, become key processes influencing the abundance and identities of species comprising the communities in each patch (Zang et al. 2005).

The concept of patch dynamics was explicitly described by Pickett and White (1985) and can be defined as a relatively discrete spatial pattern in relationship with the surrounding unaffected, or less affected matrix, and emphasizes temporal changes between spatial patches created by disturbances. The exact definition of what constitutes a patch will be relative to the system at hand. In intertidal and subtidal rocky shores (Pickett & White 1985) patches are normally created with the opening up of free space, a common limiting resource for species living here (Connell & Keough 1985).

There are many different mechanisms that can produce a patch within a community, like the ones seen on rocky intertidal shores. Disturbances from abiotic sources (see section 1.6.1) are one of the most important mechanisms and they can encompass a wide range of processes including storms, wave action, impaction, ice scouring, pollution and habitat destruction through the building of infrastructure. Biotic sources that have the potential to create patches include predation, grazing and competition. Whatever the mechanism creating the patch, they can occur over wide temporal and spatial scales, and can range from small frequent openings to rare events where large areas are cleared (Connell & Keough 1985).

Once a patch is cleared the successional state of that particular area is reset. Wright et al (2004) proposed a model of the life cycle of patches within a landscape, and they suggested there were three stages involved in this cycle. For the sake of clarity I will use an example of disturbances occurring on the rocky shore here. After the initial disturbance (e.g. a severe storm) the patch has

moved from an 'active' state to a 'degraded' state by the process of clearing. The patch then undergoes a period of recovery (unless there is another disturbance) where it now enters into a 'potential' state, as the patch once again becomes colonised it moves back into an 'active' state (Fig. 1.5).

The process of recovery of a degraded patch will initially depend on its original position and the extent of the damage caused by the disturbance event, for example, whether the patch is embedded in the matrix of the surrounding community or whether it has become completely isolated. In the case of an embedded patch the vegetative growth of survivors on the edge of the patch is the most likely and important method of re-colonisation into the patch, but in the case of an isolated area the colonisation by propagules arriving from outside of the area is more likely to be important (Connell & Keough 1985).

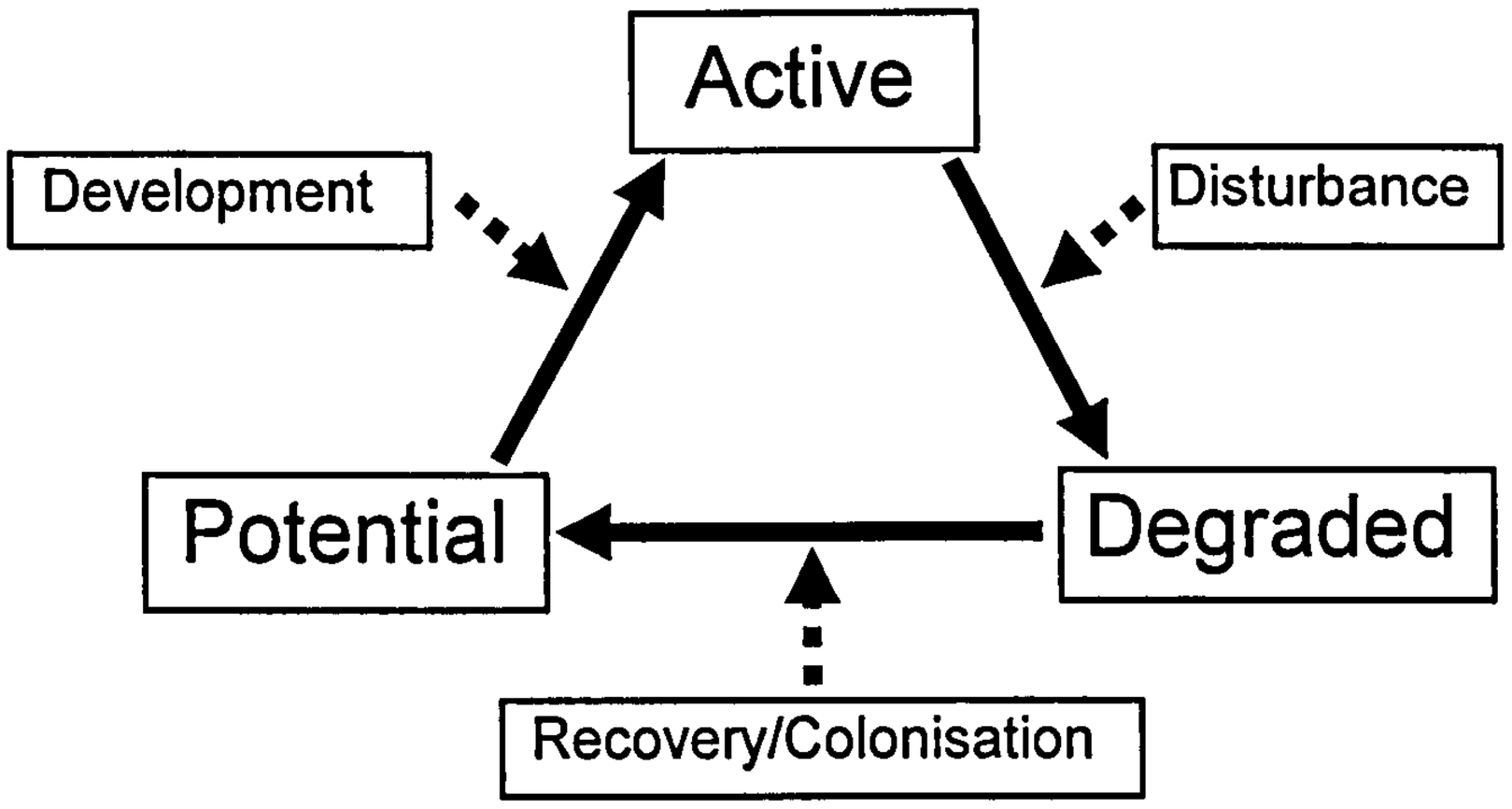


Figure 1.5 – Development of habitat patches: the different stages of community development are shown; once a disturbance impacts a community the patch is in a degraded state, the freeing up of resources that has been created by the disturbance allows recovery and colonisation into the patch which then enters into a potential state, and once the development of the community occurs the patch returns to an active state (adapted from Wright et al. 2004).

However it is important to note here that the re-colonisation of a patch is strongly dependent upon its temporal occurrence coinciding with particular recruitment patterns of individual native species as well as the recruitment periods of introduced species. For example, if an introduced species is struggling to gain a foothold in a community due to lack of competitive ability, and the community experiences a severe disturbance event which creates large patches, this may provide the opportunity for the introduced species to rapidly expand within that community, possibly preventing the native species from regaining the area, resulting in a phase shift within the community.

1.6.1 – Disturbances

Although the interaction between a number of local processes are important for the maintenance of species diversity (see section 1.5), within these local processes disturbances are one of the most significant factors. They have long been recognised as important in influencing the structure and dynamics within a community (Ayling 1981, Sousa 1984). Emphasis has also shifted from the viewpoint that disturbances are rare and unpredictable events, to treating them as natural processes that occur at different spatial and temporal scales in most ecosystems (Connell 1978). A disturbance may affect each level of organisation from the individual to the ecosystem to the landscape, and each different hierarchical level is affected in different ways (Allen & Starr 1982). Disturbances occur on wide spatial and temporal scales and their consequences are strongly dependant upon a variety of abiotic and biotic factors (Pickett et al. 1989).

There are many definitions of what actually constitutes a disturbance event (Grime 1977, White & Pickett 1985, McGuinness 1987, Menge & Sutherland 1987, Lake et al. 1989, Petraitis et al. 1989, Pickett et al. 1989, Reynolds et al. 1993, Floder & Sommer 1999, Mackey & Currie 2000, Lenz et al. 2004) the simplest of which was first described by Grime (1977) as the 'the partial or total destruction of plant (or community) biomass'. Further explanations build on this definition and have included the destruction of biomass by external mechanical forces (Menge & Sutherland 1987), and the resultant change in availability of resources after a disturbance event (Pickett & White 1985). The nature of each

disturbance event can further be subdivided into abiotic mechanisms; the movement of air, water, ice and sediment, collision with logs and rocks, or biotic mechanisms; predation and grazing from within the community (Sousa 1984). Both the abiotic and biotic mechanisms which create disturbance events are further facilitated by external forces including hurricanes and tropical storms. The occurrence of external forces are changing through global climate change (Michener et al. 1997), increases in pollution (including dredging of marine seascapes: Gray 1997), and the overexploitation of consumers resulting in an alteration of community dynamics (Worm et al. 2002). For example the removal of certain species from a community may allow the explosion of another species to the detriment of the stability and functioning of the entire ecosystem (Keystone species concept: see Paine 1976, Piraino et al. 2002). Due to the complexity involved in characterising a disturbance event it is therefore important to define both the mechanism of disturbance and the disturbance event itself prior to experimental investigations.

1.6.2 – Productivity

Productivity is thought to be another major factor influencing local patterns of biodiversity. The supply of nutrients into a community sets the rates of primary productivity (Worm et al. 2000, Worm et al. 2002) and the transformation of this energy into organic matter ultimately governs the productivity of ecosystems (Cardinale et al. 2004). It is proposed that with an increase in production an ecosystem can support a greater diversity of species due to increased levels of energy flowing through the food web (Connell & Orias

1964). The increased levels of primary productivity mentioned can be followed through the community and up the food web by observing increased growth rates of organisms and increased rates of production of offspring, resulting in increased population sizes.

However, the concept of species diversity relating to productivity remains a contentious issue. The impact that increases in productivity alone will have on a community will depend entirely on the background levels of nutrients. In environments associated with very low productivity, nutrients are seen as a limiting resource (Proulx & Mazumder 1998). Increases in the availability of nutrients will immediately result in an increased survival and growth of several species. However this will only occur up to a point of saturation where further increases in the levels of nutrients now results in a decline of species richness due to a few species becoming favoured by the environment and out competing all others (Proulx & Mazumder 1998, Hillebrand 2003); a phenomenon which Connell and Orias (1964) termed the "community stability hypothesis" presenting a unimodal pattern of species diversity (Waide et al 1999). Productivity, however, rarely occurs in the absence of other local factors, if for example the effects of productivity are combined with those of disturbances the dynamic equilibrium hypothesis is applicable (Huston 1979).

1.6.3 - Spatial heterogeneity

The theory of spatial heterogeneity claims that 'the more complex and heterogeneous the physical environment becomes, the more diverse the plant and animal communities supported by that environment are'. For example the land has more niches available for colonization than the sea, and the tropics more niches than temperate areas (see mechanisms of species diversity: Connell & Orias 1964). Habitat complexity was named as one of the mechanisms with which high levels of diversity were maintained under equilibrium models of species diversity.

Island biogeography theory (MacArthur & Wilson 1967) states that larger areas support more species; the spatial heterogeneity of these areas is thought to enhance community development by providing a diversity of microhabitats (Soniat et al. 2004). In topographically complex habitats, such as those found on rocky shores, pits and crevices are thought to provide refuges for sessile invertebrates against biotic and abiotic disturbances (Walters & Wethey 1996), and they have been shown to reduce catastrophic losses that have occurred due to these forces (Connell 1961). The peaks that are associated with the pits and crevices also provide a refuge for other organisms, generally those with poor competitive abilities can find refuges on the peaks of these topographies because they are less desirable places to settle with less protection to strong environmental forces (Anderson & Underwood 1994, Guichard et al. 2001).

Habitat complexity changes the physical characteristics of the environment, through for example the mediation of water flow at high tide and shading and/or air flow at low tide (Guichard et al. 2001). Biological characteristics, such as growth through food flux for suspension feeders, recruitment through larval supply, maximum body sizes (Gaylord et al. 2001) and post settlement mortality (Connell 1961) which are all mediated by hydrodynamic forces (Guichard et al. 2001) are also influenced.

1.7 - Conclusion

Understanding the determinants that control patterns of species diversity, alongside an understanding of the mechanisms that allow the co-existence of species, will better enable the discovery of how the role of biodiversity is important to ecosystem processes, and ultimately to how they will respond to the numerous effects of global environmental change.

At present the Earth is undergoing massive environmental changes due primarily to anthropogenic global change, and natural processes which are integral in maintaining species co-existence within ecosystems are thought to be affected. Disturbances are one of the most important factors in maintaining the co-existence of species, and though there are many definitions of what constitutes a disturbance, their frequency, intensity and timing are all thought to increase as a direct consequence of the anthropogenic changes outlined herein. This could have severe consequences for the biodiversity that they currently maintain. With rapidly shifting disturbance regimes many species may not be

able to adapt and may subsequently be lost from the system, having potentially damaging consequences for their survival and the survival of the ecosystem in question.

1.8 – Aims and thesis summary

The aim of this thesis was to focus on the specific local scale processes that are thought to drive the co-existence of species within community assemblages. Although it is agreed that large regional scale processes are fundamentally important to the species pool (those species that are potentially able to exist within a community assemblage), investigating them was beyond the scope of the experiments described here. The primary goal was therefore to investigate disturbances in temperate benthic subtidal habitats, and secondary aims incorporated the interactions between disturbances, productivity and habitat complexity. All experimental work was conducted in the field to maximise the relevance of results to complex natural systems. The structure of the experimental chapters is as follows:

Chapter Two: The influence of nutrient enrichment and disturbance frequency on the diversity of temperate benthic marine communities.

The aims were to determine whether physical disturbances affected species diversity and community compositions in sessile benthic communities of two different successional stages, as an experimental test of the Intermediate Disturbance Hypothesis as proposed by Connell (1978). This study then went

on to investigate whether different levels of nutrient availability interacted with disturbance frequency to influence the point at which maximum species diversity was found. This attempted to determine whether disturbance productivity interactions were important for the diversity and structure of these subtidal communities.

Chapter Three: The temporal variability of disturbance regimes: Is this important for the diversity and composition of benthic subtidal assemblages?

Once it was established that disturbances were important forces in structuring subtidal communities, the frequency of disturbance events over time was fixed and the timing of events was manipulated to produce a series of disturbance events that were either clustered together or spaced apart in order to investigate whether the temporal variability of disturbances regimes influenced species diversity or the composition of these communities.

Chapter Four: The effects of surface complexity in providing refuges for benthic marine communities against abiotic disturbances

Disturbances are important forces structuring the composition of benthic marine organisms in temperate areas. The frequency, intensity and timing of these disturbances are thought to be affected by global change, and with growing human populations urbanisation of the World's coastline is thought to increase. This study aimed to investigate the value of specific microhabitats within larger

scales of surface complexity, and to discover whether particular species preferred to settle in specific microhabitats. It also aimed to determine whether different types of disturbances affected subtidal and intertidal sessile communities in the same way, as well as attempting to determine whether more complex surfaces provided refuges against the different types of disturbances imposed on them.

Chapter Two: The influence of nutrient enrichment and disturbance frequency on the diversity of temperate benthic marine communities.

2.1 - Introduction

The factors and mechanisms which control patterns of biodiversity have long been debated, with the development of many hypotheses (Huston 1994, Rosenzweig 1995, Collins & Glenn 1997). It is now generally accepted that conditions within ecosystems are continually changing, and interacting factors at local scales influence biodiversity. Identified as important factors are the natural history of a community, local climate, predation, competition, productivity, disturbances and spatial/habitat heterogeneity (Krebs 2001, Johnson et al. 2003, Mittelbach et al. 2007). In this study we chose to examine the interaction between disturbance frequency and nutrient input. Both of which are increasing due to anthropogenic change (Smith & Buddermeier 1992, Michener et al. 1997, Espinosa et al. 2007).

The intermediate disturbance hypothesis (IDH; Connell 1978) is a non-equilibrium model of species diversity, and it contributes to the widely accepted viewpoint that communities rarely reach equilibrium (Collins and Glenn 1997). The IDH predicts that diversity will be maximised in communities experiencing intermediate levels of disturbance. If disturbances are too rare, competitive dominants will eliminate subordinate species and reduce the diversity because stable conditions develop. If disturbances are too frequent, most species will go locally extinct because they cannot tolerate the repeated disturbances, therefore reducing diversity. Under intermediate levels of disturbance, diversity is maximised because disturbance tolerant species and competitively dominant species co-exist producing a unimodal pattern of species diversity (Connell

1978). However, although widely accepted a review of studies on the IDH by Mackey and Currie (2001) revealed that only 15 % supported this unimodal pattern. This suggests the need for more extensive research in this area, in a range of different habitats, with consideration of interactions with other factors, such as productivity.

It has been suggested that the absolute diversity of a system is dependant upon nutrient import and the amount of energy flowing through a system (Paine 1966). Consequently, productivity has a major influence on biodiversity, as well as controlling the rates of competitive exclusion and recovery after a disturbance (Abrams 1995). Increased productivity means an increased growth rate of all species, which leads to increased competitive exclusion. This ultimately results in lower species diversity and decreased spatial heterogeneity of limiting resources (Abrams 1995). Conversely, it has been argued that in aquatic systems increased availability of nutrients favours both algal and sessile invertebrate species, which can result in a phase shift between the foundation members of a community and indirectly affect biodiversity. For example, by simply adding structure and colonisation area through enhanced growth, the resulting increased habitat heterogeneity will have a knock-on effect on biodiversity (Proulx & Mazumder 1998, Kondoh 2001, Hillebrand 2003, McAbendroth et al. 2005). In temperate rocky intertidal and subtidal systems good examples of this effect can be found in mussel beds (Seed 1996, Ricciardi et al. 1997) and in the interaction between algal and macro-invertebrate diversity (Begin et al. 2004). There will be other ways in which disturbance and productivity interact to change biodiversity, and although disturbances themselves can have strong effects on species diversity (Mackey & Currie

2001), it has been suggested that the diversity-disturbance relationship can be positive or negative, depending on the productivity of the system (Kondoh 2001). Productivity is also thought to influence the peaked unimodal pattern predicted by the IDH (Dynamic equilibrium model: Huston 1994, Kondoh 2001), by increasing the growth rate of competitive dominants.

Communities established on artificial settlement panels at two different successional stages were used to investigate the interactive effects of nutrient availability and disturbance frequency, and to test the hypothesis that, 'an increase in nutrient availability will increase the disturbance frequency at which maximal diversity is found'. Experiments were carried out in the field using subtidal benthic communities because they provide systems amenable for ecological studies, due to rapid settlement and establishment on free space, which is considered to be a limiting resource, as well as year round recruitment and fast recovery after disturbances (Bertocci et al. 2005). Increased diversity found in some more mature marine benthic communities has been shown to increase resilience to disturbances (Tilman et al. 2006, Worm et al. 2006). Therefore we used two different successional stages of community, by placing artificial panels into the water at different times of the year, in our model system to discover whether more mature benthic communities promoted resilience to disturbances.

2.2 – Materials and Methods

2.2.1 – Site Description

Experiments were carried out between February and October 2004 in Hartlepool Marina, on the North East coast of England (N – 54° 41' 556'', W – 001° 12' 015''; Fig. 2.1). The marina is non-tidal as it is fully enclosed serving as a natural mesocosm where communities persist in a relatively sheltered environment compared to that of an exposed rocky shore where physical disturbances frequently occur. Communities within the marina were therefore very susceptible to the treatments being applied in this sheltered habitat. There is no freshwater input (other than rainwater) and salinity was 35 ppt. Temperature ranged from 6 ^{0}C in the winter to 20 ^{0}C in mid-summer (Fig. 2.2). The established benthic community in the marina is diverse with up to 20 sessile and 15 mobile species observed.

Figure 2.1– Map of Great Britain (a) with the location of Hartlepool shown by the black dot, and b) map of the marina showing clearly the lock gate through which water exchange occurs.

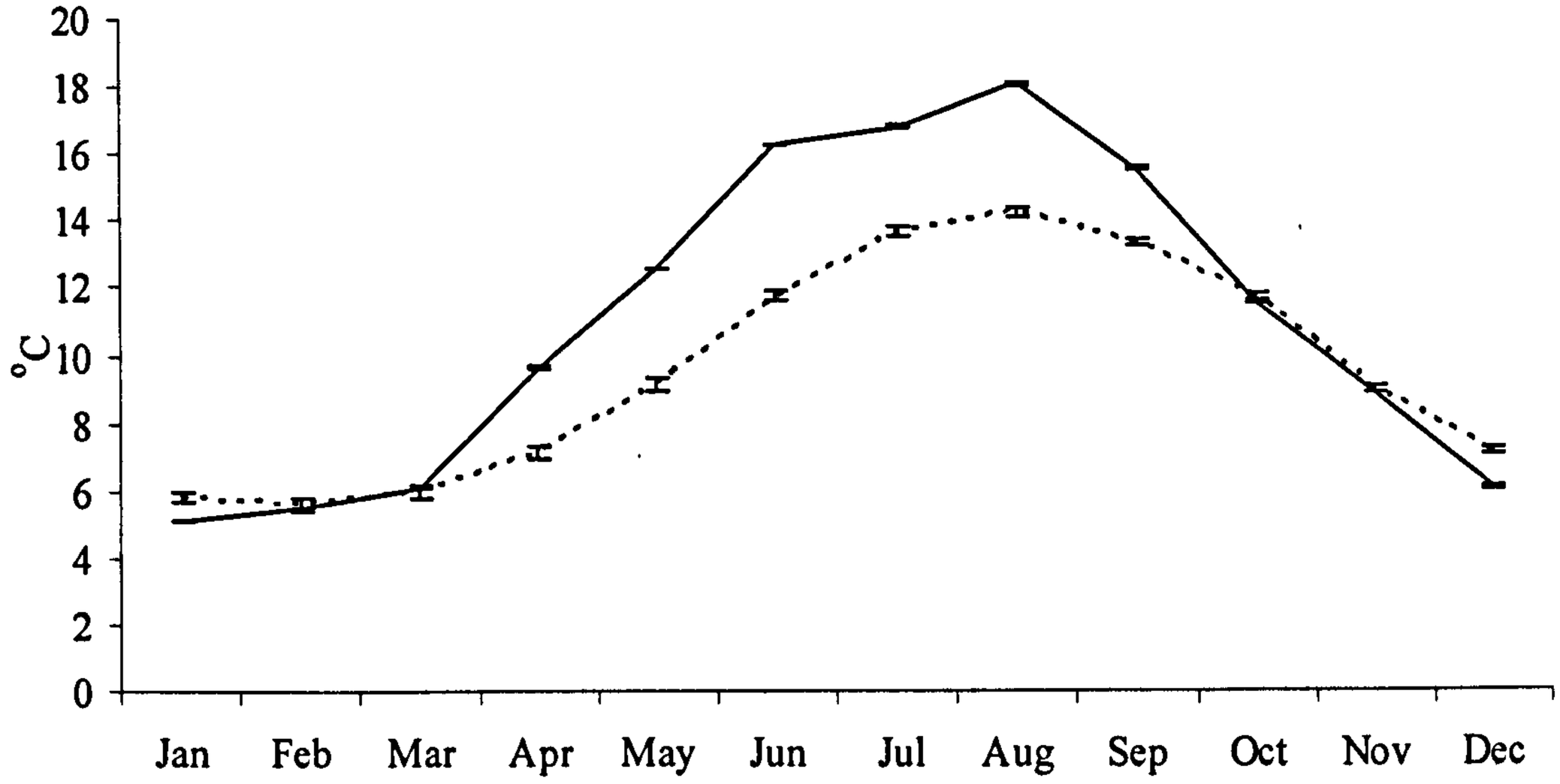


Figure 2.2 – Monthly mean sea surface temperatures (+- SE) within Hartlepool marina (solid line) and in open coastal waters at Redcar (N 54° 37', W 1° 4', dotted line). Marina data span 2002 to 2005 (n = 20868) and Redcar data span 1961 to 2000 (n = 27 per month, CEFAS data).

2.2.2 – Experimental Approach

Roughened grey PVC panels (15 x 15 x 0.3 cm, Bay Plastics Ltd) were used as artificial settlement substrata. Roughening was standardised using a sander (Metabo, SXE 425) with sand paper (P60 grit paper) for 10 seconds/panel. Settlement panels were arranged vertically in a single row on rings constructed from PVC strips (205 x 25 x 0.3 cm). Panels were fixed reversibly to these rings with cable ties (100 x 2.5 mm) to allow the return of panels after sampling. The final result can be seen in Fig. 2.3.

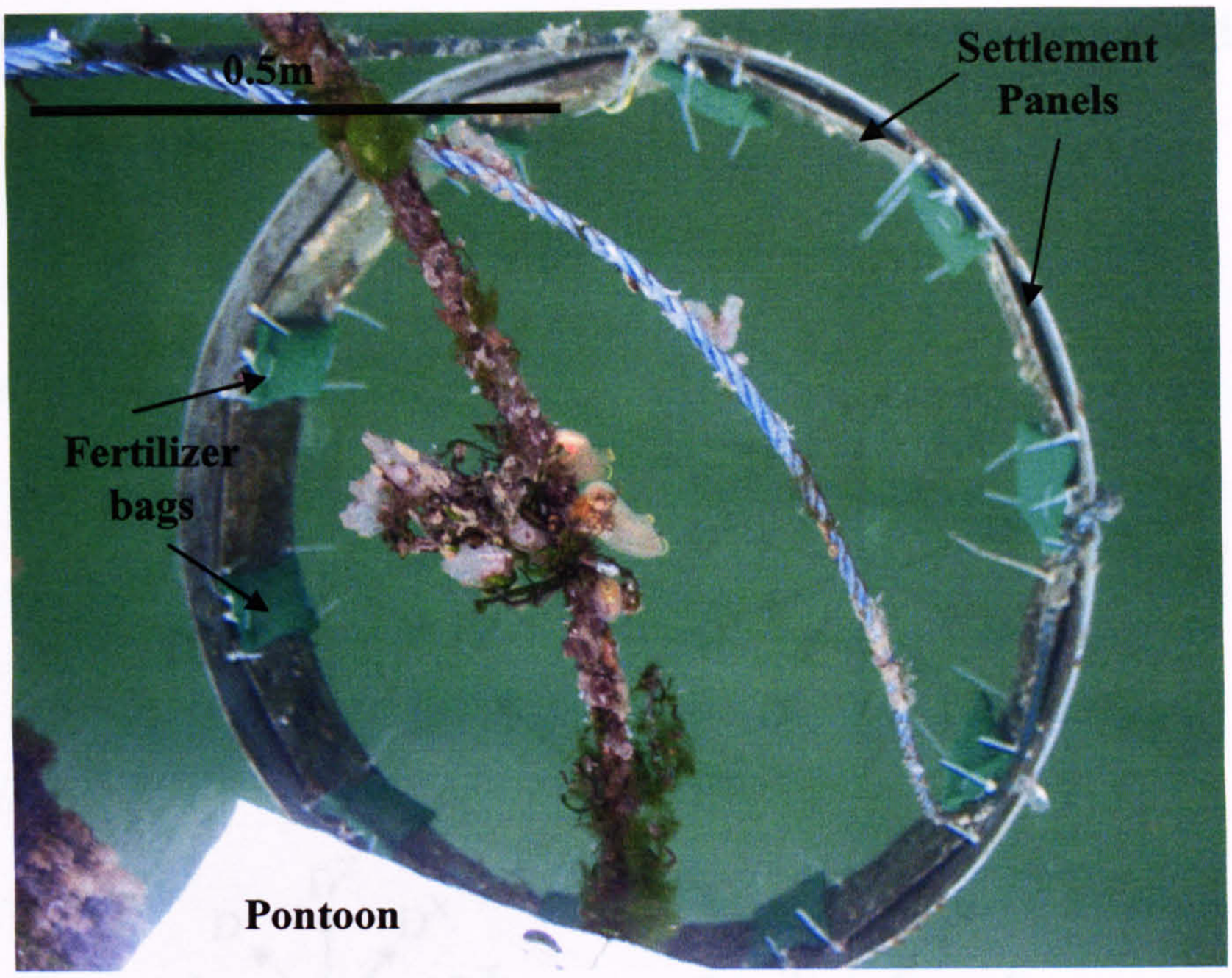


Figure 2.3 – Completed ring, showing attached settlement panels and fertilizer bags, hanging beneath pontoons.

The experimental approach was a three-factorial nested design following Worm et al. (2002), where nutrient availability (3 levels) and disturbance frequency (7 levels) were fixed factors, and ring was a random factor, with nutrient availability nested within ring (Fig.2.4). One ring had one level of nutrient availability; each level was replicated four times. The experiment was separated into two main phases. During the maturing phase half (n = 120) of the settlement panels were submerged at 50 cm to allow natural colonisation of the panels for three months (February to May): these produced the mature communities. After this maturing phase the remaining settlement panels (n = 120) were deployed in May to create the non-mature communities. Thereafter,

all the panels (n = 240) were manipulated with different nutrient availability and disturbance frequencies for 24 weeks.

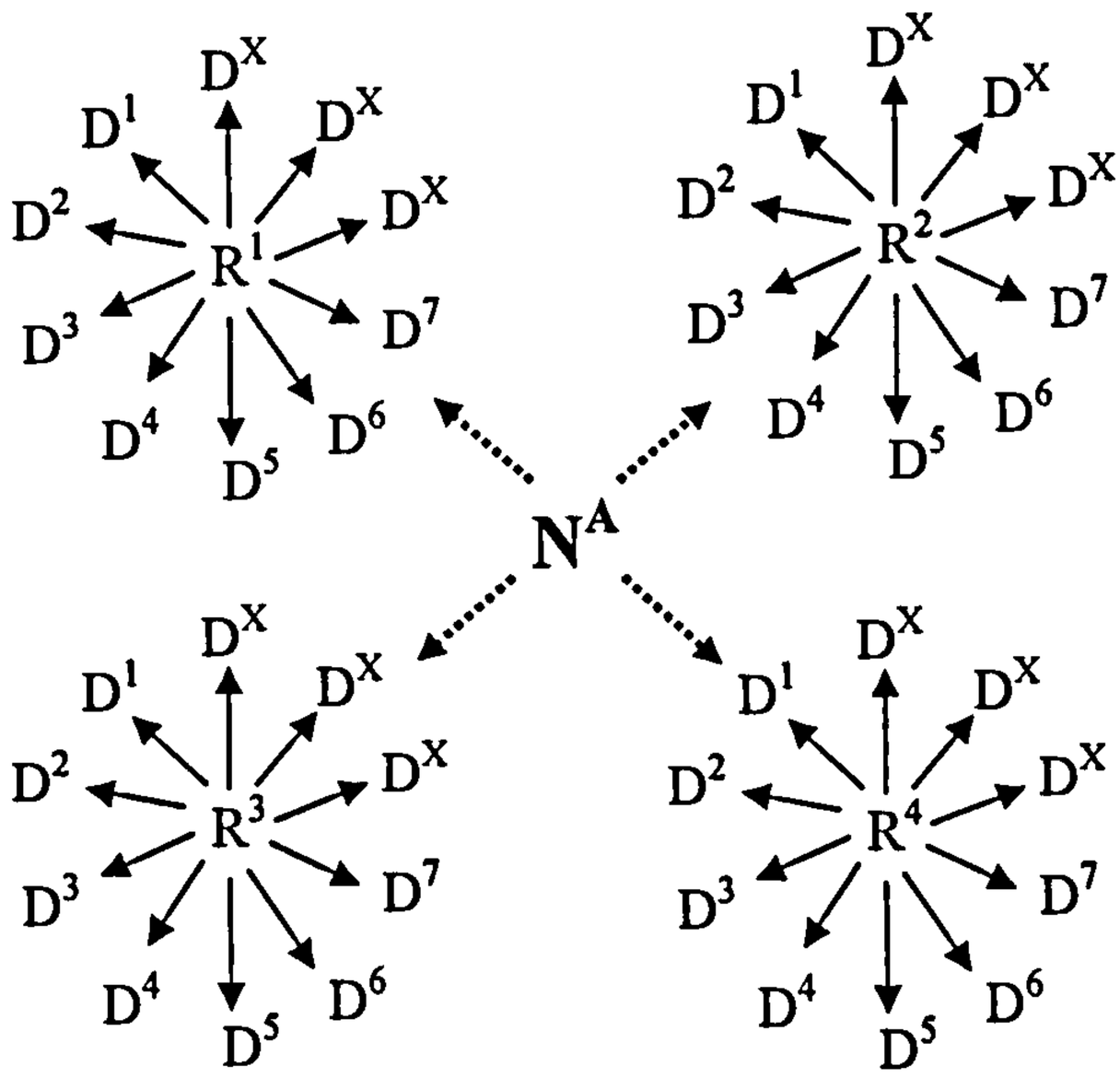


Figure 2.4 - Schematic diagram representing the nesting of factors within a level of nutrient enrichment where NA represents ambient nutrients, R represents the ring (1-4) and D the level of disturbance frequency (1-7) within each ring. D^X represents the random allocation of a disturbance treatment within a ring. This set up is repeated for both enriched and super enriched levels of nutrient enrichment.

2.2.3 – Nutrient Availability

Nutrient availability was achieved using Plantacote PLUSS 6M coated-controlled release fertiliser which provided gradual nutrient release allowing for realistic nutrient gradients and even application (Worm et al, 2000). Bags (15 cm x 3 cm) of fertilizer constructed of 1 mm polyethylene mesh were attached to rings, with 10 bags per ring, each next to a panel (Fig 2.3). Rings were then randomly arranged in a line across the marina from floating pontoons, with 5 metres separating each ring, at a constant depth of 50 cm.

Three levels of nutrient availability were used to manipulate the levels of nutrients available for uptake by communities. Nutrient levels were ambient (pebbles were added to the bags to keep hydrodynamic conditions around panels the same), enriched (100 g of fertilizer added which raised the ambient concentration by ~50 %), and super-enriched (200 g of fertilizer added which raised the ambient concentration by ~100 %). Values of nutrient availability were determined during pilot studies, Chlorophyll a was measured to determine nutrient levels (ambient; 0.11μm/l SD - 0, enriched 0.57μm/l SD – 0.32, super-enriched 1.2μm/l SD – 0.24) as an indicator of productivity, and fertilizer was renewed every four weeks to maintain constant levels of enrichment.

2.2.4 - Disturbance Treatments

Disturbance treatments were carried out over the experimental time period at different intervals to provide a gradient between frequent and rare disturbance events. There were seven frequency levels and these consisted of no disturbance (as a control), and disturbance every 12^{th}, 10^{th}, 8^{th}, 6^{th}, 4^{th} and 2^{nd} weeks. The same disturbance treatments were carried out in each level of nutrient availability, with 4 or 5 replicates of each combination (see below). The area to be disturbed was selected randomly and all of the biomass in this area was removed. Each experimental unit was disturbed in two separate areas during a single disturbance event, each 10 % area of the panel (Fig. 2.5). Two separate areas were used to reduce the chances of entirely destroying one organism in the community and a 20 % disturbance area was used to mimic the intensity of naturally occurring disturbances in this type of habitat (Dayton 1971, Povey & Keough 1991).

Figure 2.5 – Recently disturbed settlement panel covered with Ectocarpus siliculosus, Ascidiella aspersa *and green algae, with black circles showing areas where biomass has recently been removed.*

All disturbance treatments were present in each ring and their position within the ring was allocated randomly, this filled seven settlement panels within each ring (Fig. 2.6). Three settlement panels remained without a disturbance treatment. These panels were grouped across nutrient enrichment treatments (i.e. four rings in each) and a within ring replicate of each treatment was randomly assigned. In this way it was ensured that every disturbance treatment was replicated at least once within a ring in the same nutrient treatment. On the remaining five settlement panels a second within ring replication of a randomly chosen treatment was assigned. The final set up consisted of twelve rings with mature communities and twelve rings with non-mature communities.

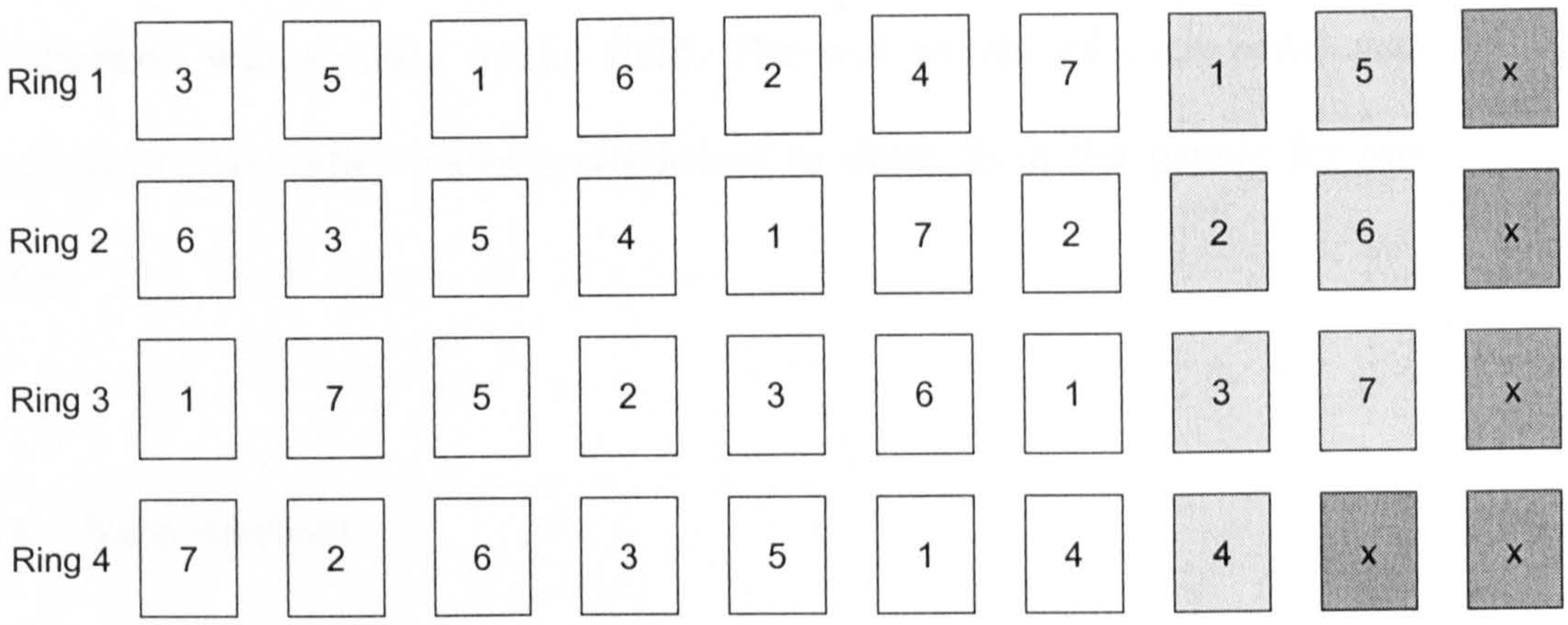


Figure 2.6 - Arrangement of settlement panels on rings. Rings 1-4 represent one level of nutrient enrichment replicated four times. Numbers 1-7 represent the seven disturbance treatments allocated to each ring, while light grey panels represent the within ring replication of each disturbance treatment. Dark grey panels represent the second within ring replication of five randomly chosen disturbance treatments.

2.2.5 - Sampling

Each panel was photographed at the beginning of the treatment phase and then every month (Canon G3 Powershot, 4 x 10^6 pixels). Pictures were downloaded in Canon RAW format to maintain resolution using Canon Zoombrowser and analysed as 8 bit TIFF files. Percent cover of species was estimated using ImageJ version 1.32j using colour threshold and overlaid points (Meese & Tomich 1992, Dethier et al. 1993). The colour threshold method was used initially with simple communities comprised of barnacles, however with a more complex community quickly becoming established the overlaid point method

was used. A 1 cm edge was left un-sampled to reduce edge effects. Species identification was verified in the field. The wet weight of each panel was measured (+/- 1g) after water was allowed to drain from the panels for one minute.

2.2.6 – Data Analysis

Biomass, using wet weight, and the total abundance were measured and diversity (Shannon index, H'), species richness, evenness were calculated (Magurran 1988). Missing value analysis was performed to estimate the values of two lost panels using regression. Prior to analysis, data was transformed with the Box-Cox transformation using optimal lambda values in order to meet parametric assumptions using Minitab 12.2.

To test for significant interactions between nutrient availability and disturbance frequency, as well as the main effects of the two treatments, a three factorial crossed and nested ANOVA was done following the model;

$$X_{ijkl} = \mu + N_i + R(N)_{j(i)} + D_k + N_i \times D_k + D_k \times R(N)_{j(i)} + e_{l(ijk)}$$

Where X_{ijkl} represents the variable of experimental unit *l* that is characterised by disturbance *k*, nutrient enrichment *i*, and is located on ring *j*. μ is the mean of the variable X. e represents the error due to the smaller scale differences between samples because of spatial variability within a ring, also known as residuals. N (nutrient enrichment), D (disturbance) and R (ring), if they exist represent the

effects of the treatments. X represents the crossing of factors while brackets represent the nesting of factors (Underwood, 1997). Due to the random allocation of replicated disturbance treatment across rings within nutrient treatments resulting in an unbalanced design, the variance components were calculated using dummy variables in Statistica. Dummy variables were assigned to the replicate of each treatment, so for example replicate 1 received a 1, replicate 2 a 2 and so on. Dummies 1 and 2 were used to calculate the main ANOVA whilst dummies 2 and 3 were used to calculate the error term (full details of the calculated variance components are given in Table 2.1). Due to the unbalanced design and the necessity of building the final ANOVA from constituent variance components, it was not possible to analyse a repeated measures model. Therefore to examine changes in the response variables over time a separate ANOVA was run for each sampling date and sequential Bonferroni adaptation was used to reduce the risk of type 1 errors (Holm 1979). Tukey's HSD *post hoc* analysis was used to examine the significant effects of disturbances (using the ANOVA error term), whilst in the presence of significant interactions *a priori* quadratic and linear contrasts were performed to discover if the interaction fit the model proposed by Kondoh (2001).

Table 2.1 –The inclusion of dummy variables (1, 2, 3) in the calculation of the nested ANOVA where nutrient availability = N, Ring = R, Disturbance frequency = D represent the sources of variation.

Source of Variation	Effect	SS	df	MS	Denominator for F
N	Fixed	1 & 2	1 & 2	1 & 2	R(P)
R(N)	Random	1 & 2	1 & 2	1 & 2	Error
D	Fixed	1 & 2	1 & 2	1 & 2	D x R(N)
D x N	Fixed	1 & 2	1 & 2	1 & 2	D x R(N)
D x R(N)	Random	1 & 2	1 & 2	1 & 2	Error
Error		2 & 3	2 & 3	2 & 3	

In order to view changes in the natural communities over time, Discriminant cluster analyses were carried out using data on the percentage cover of species. This uses a linear ordination of the F-statistic and identifies homogeneous subgroups of species within the population identifying a set of groups which minimise within-group variation but maximise between-group variation (Field 2000). Multi-dimensional scaling (MDS) ordinations, based on Bray Curtis similarity co-efficient calculated from square root transformed, non-standardised data, were used to compare differences between communities at the different successional stages. With the intention of comparing differences between community compositions at the different treatment levels a one way Analysis of Similarity (ANOSIM) was done on the square root transformed, non-standardised data. Similarity Percentage Analysis (SIMPER), using the square root transformation identified which species contributed most to the observed dissimilarities. Statistics were carried out using SPSS V11.5, Statistica V6, Minitab V14 and Primer V5.

2.3 – Results

2.3.1 – Community Composition

Multi-dimensional scaling (MDS) plots show the communities of the two successional stages had some differences from the onset of the experiment (Fig. 2.7a) and that the communities continued to diverge with time, the differences becoming greater at 12 weeks (Fig. 2.7b). At 24 weeks the two communities were different from one another (Fig. 2.7c) with different species comprising the majority of the community. Although stress values (all <0.1) represent good ordinations of the plots, conclusions were validated with ANOSIM which confirmed significant dissimilarities (4 weeks; $R^2 = 0.38$ P <0.001, 12 weeks; R^2 = 0.69 P <0.001, 24 weeks; R2 = 0.41 P <0.001), and SIMPER analyses attributed these differences mostly to contributions by *E. siliculosus* (16%), *Balanus crenatus* (16%), *A. aspersa* (14%) and *Cladophora rupestris* (14%).

A total of fourteen species were found in the experimental communities, their appearances during the experimental phase are documented in Table 2.2 (a-b). In the mature communities, a temporal ANOSIM showed that the communities were significantly different from all other communities at 12 weeks, differences were attributable to contributions of *E. siliculosus* (contributing to a dissimilarity of 30 %, SIMPER analysis). There were no significant differences between the communities during the first or the final weeks of sampling (Table 2.3). Cluster diagrams show the community evolving in a clockwise rotation,

beginning and ending with mostly solitary ascidians, but becoming more diverse in week twelve with colonial species present (Fig. 2.8, Table 2.4).

The non-mature communities show some significant differences from the onset of the treatment phase with differences becoming greater at weeks 12 and 16. These differences are attributable to the contributions by *E. siliculosus, B. leachi, Botryllus schlosseri* and *Bugula flabellata*, (contributing to a dissimilarity >50%, SIMPER analysis). In the final weeks of the sampling the communities are once again similar (Table 2.2). Cluster diagrams show that the community evolves in an anti-clockwise rotation beginning and ending with colonial species but becoming more diverse in week twelve with solitary species present (Fig. 2.8, Table 2.4).

Table 2.2 a. - List of Species grouped by phylum found in the mature communities. Appearance of organisms shown by ○: not present, ●: ≤ %-rare, ●●: <10% cover, ●●●: >10% cover.

	Abundance After:						
Algae	0 weeks	4 weeks	8 weeks	12 weeks	16 weeks	20 weeks	24 weeks
Chlorophyta							
Cladophora rupestris ((Linnaeus) Kűtzing)	●●●	●●	●●●	●	●●●	●●	●
Ulva lactuca (Linnaeus)	○	○	●	●	●	●	●
Chromophycota							
Ectocarpus siliculosus ((Dillwyn) Lyngbye)	●●●	●●●	●●●	●●●	●●	●●●	●●
Rhodophyta							
Ceramium rubrum (Hudson)	○	○	●	●	●	●	●
Animals							
Annelida							
Pomotoceros triquieter (Linnaeus)	○	○	●	●	●	●	●
Arthropoda							
Balanus crenatus (Brugiere)	●●●	●●●	●●●	●●●	●●●	●●●	●●●
Bryozoa							
Bugula flabellata (Thompson in Gray)	○	○	○	●	●●	●●	●●
Umbonula littoralis (Hastings)	○	○	○	●	●	●	●
Chordata – Ascidians							
Ascidiella aspersa (O F Műller)	○	○	●●	●●●	●●●	●●●	●●
Botrylloides leachi (Savigny)	○	○	●	●●●	●●●	●●●	●●
Botryllus schlosseri (Pallas)	○	○	●	●●	●●	●●	●
Ciona intestinalis (Linnaeus)	○	○	●●	●●	●●	●●	●●
Clavelina lepadiformis (Műller)	○	○	○	●●	●	●	●
Mollusca							
Mytilus edulus (Linnaeus)	○	○	●	●	●	●	●

Table 2.2 b. - List of Species grouped by phylum found in the non-mature communities. Appearance of organisms shown by ○: not present, ●: ≤ %-rare, ●●: <10% cover, ●●●: >10% cover.

	Abundance After:						
Algae	0 weeks	4 weeks	8 weeks	12 weeks	16 weeks	20 weeks	24 weeks
Chlorophyta							
Cladophora rupestris ((Linnaeus) Kűtzing)	○	●●●	●●	●●	●●●	●●	●
Ulva lactuca (Linnaeus)	○	○	○	○	●	●	●
Chromophycota							
Ectocarpus siliculosus ((Dillwyn) Lyngbye)	○	●●●	●●●	●●●	●	●●●	●●●
Rhodophyta							
Ceramium rubrum (Hudson)	○	○	●	●	●	●	●
Animals							
Annelida							
Pomotoceros triquieter (Linnaeus)	○	○	●	●	●	●	●
Arthropoda							
Balanus crenatus (Brugiere)	○	○	○	●	●	●	●
Bryozoa							
Bugula flabellata (Thompson in Gray)	○	○	●	●●	●●	●●	●●
Umbonula littoralis (Hastings)	○	○	○	○	●	●	●
Chordata – Ascidians							
Ascidiella aspersa (O F Műller)	○	●	●	●●	●●	●●	●●
Botrylloides leachi (Savigny)	○	●	●	●●●	●●●	●●	●●
Botryllus schlosseri (Pallas)	○	○	●●	●●	●●	●●	●
Ciona intestinalis (Linnaeus)	○	●	●	●	●●	●●	●●
Clavelina lepadiformis (Műller)	○	○	●	●●	●	●	●
Mollusca							
Mytilus edulus (Linnaeus)	○	○	○	○	○	●	●

Table 2.3 – ANOSIM comparing natural communities over the experimental period, based on Bray Curtis similarity and square root transformation.

Sampling Session	Mature Communities R^2	Mature Communities Significance Level %	Non mature communities R^2	Non mature communities Significance Level %
1-2	-0.02	ns	0.406	0.2
1-3	0.689	0.1	0.719	0.1
1-4	0.762	0.1	0.831	0.2
1-5	0.766	0.1	0.719	0.2
1-6	0.725	0.1	0.77	0.1
2-3	0.706	0.1	0.844	0.1
2-4	0.965	0.1	0.807	0.1
2-5	0.954	0.1	0.701	0.2
2-6	0.859	0.1	0.765	0.1
3-4	0.737	0.1	0.721	0.1
3-5	0.616	0.1	0.709	0.1
3-6	0.629	0.2	0.673	0.1
4-5	0.168	4.8	0.02	ns
4-6	0.183	2.6	0.022	ns
5-6	0.042	ns	-0.09	ns

*Table 2.4 – The contribution of species to the structure of the discriminant cluster analysis in mature and non-mature communities. Numbers with * contribute to the largest absolute correlation between each variable at any discriminate function, and therefore make up that function. (a. –* P. triqueter*)*

Species	Mature Communities Function One	Mature Communities Function Two	Non-Mature Communities Function One	Non-Mature Communities Function Two
A. aspersa	0.424*	0.074	0.031	0.279*
C. intestinalis	0.259*	-0.067	-0.061	-0.137
E. siliculosus	-0.509	0.799*	0.586*	0.073
B. leachi	0.277	0.412*	0.383	0.336
C. lepadiformis	0.222	0.319*	-0.035	-0.096
B. schlosseri	0.204	0.036	0.097	0.071
M. edulus	0.126	-0.141	a. -0.082	0.322*
C. rubrum	0.103	0.055	-0.061	0.001
U. littoralis	0.039	-0.108	-0.099	-0.224
B. flabellata	0.214	-0.097	-0.073	0.525*
C. rupestris	-0.203	-0.052	0.028	-0.013
B. crenatus	-0.24	-0.138	-0.05	-0.122

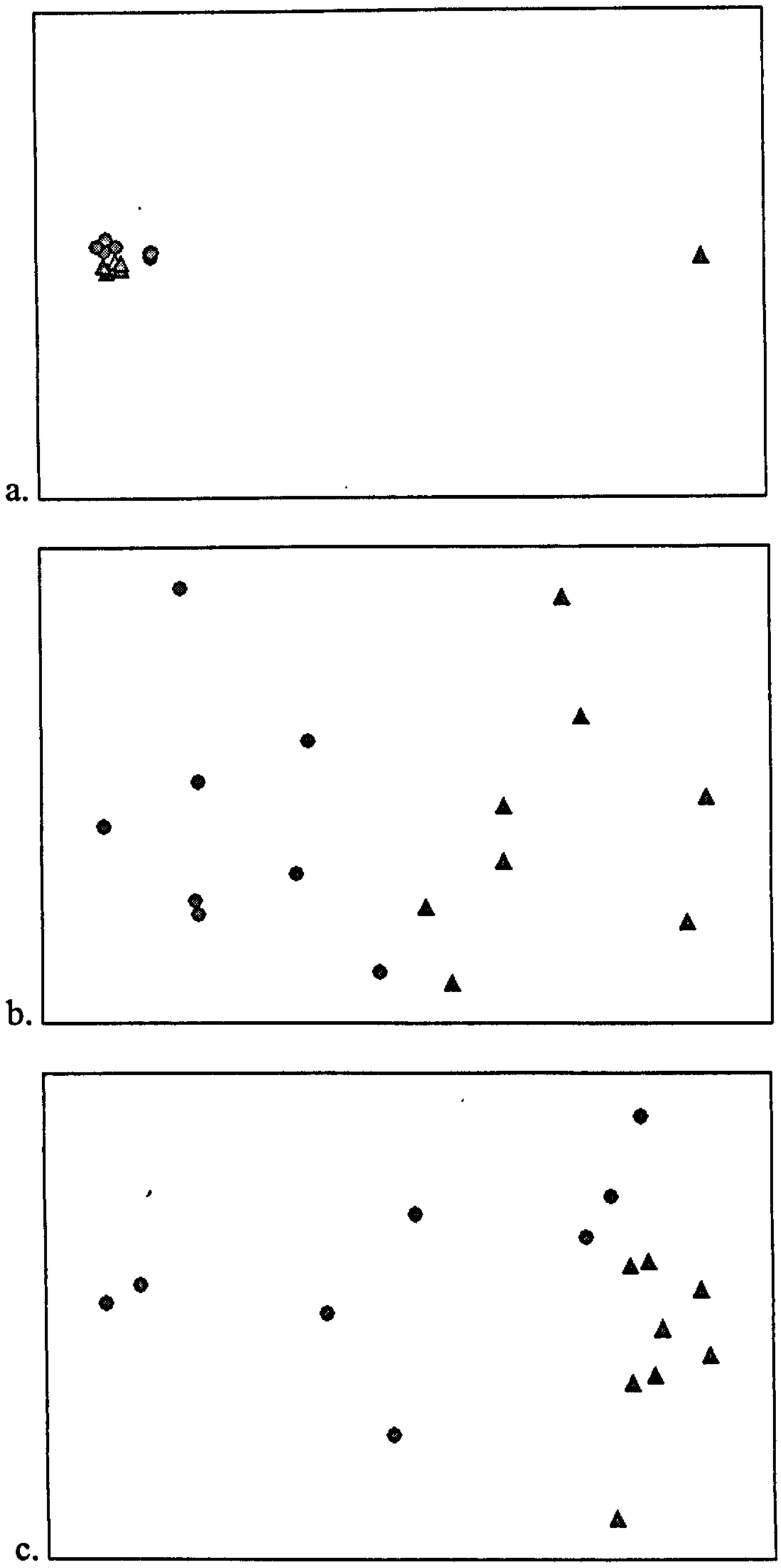


Figure 2.7 – MDS ordination of the two community stages after a. 4 weeks – stress value 0.01, b. 12 weeks – stress value 0.07 and c. 24 weeks – stress value 0.09 based on square root transformed abundances and Bray Curtis similarity. Triangles – mature communities; Circles – non-mature communities.

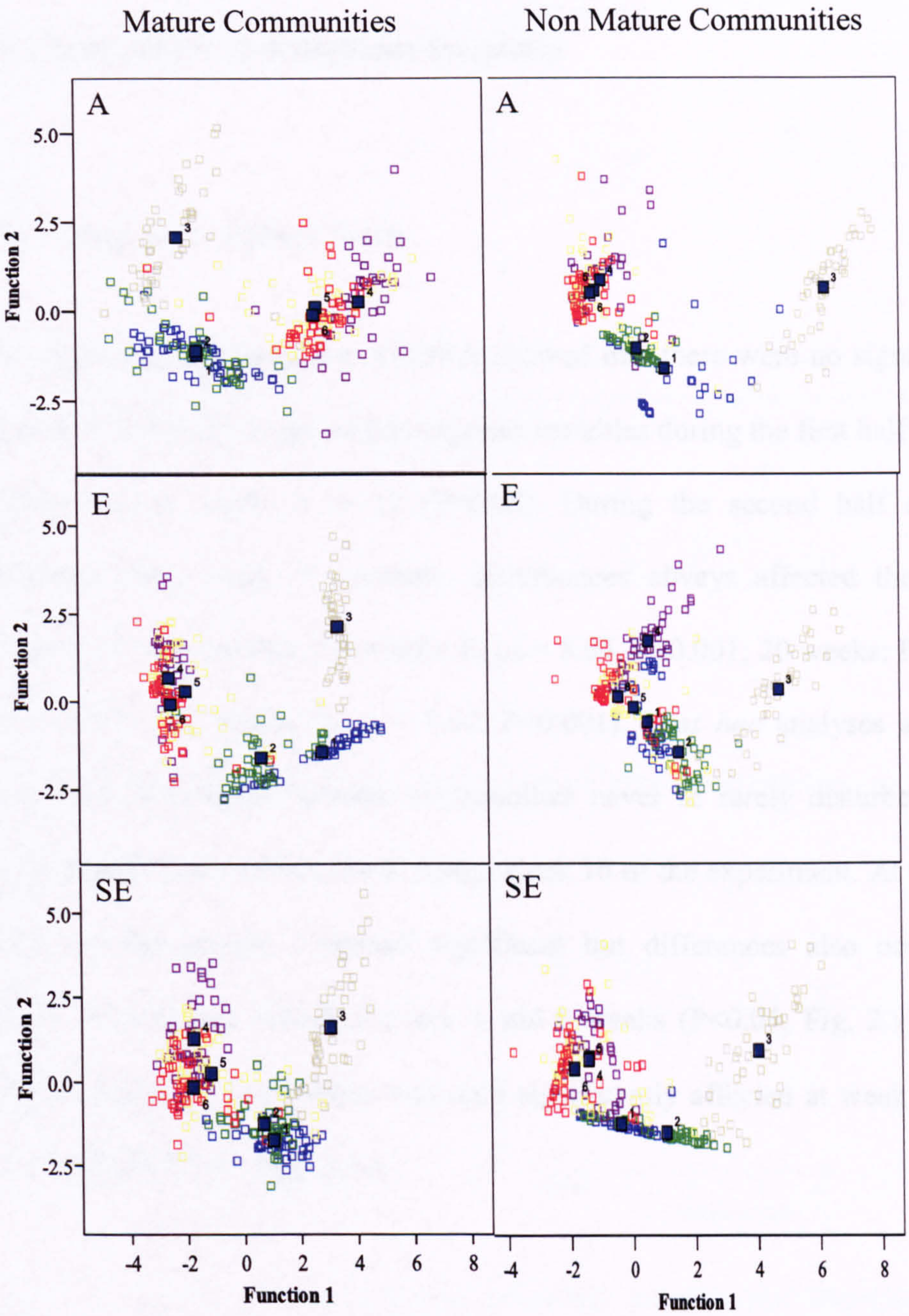


Figure 2.8 - Discriminant cluster plots showing the change in communities over the experimental phase where A – ambient, E – enriched and SE – super-enriched. Function 1 is the linear combination of variables showing the maximum number of differences between groups, and function 2 separates groups using the residual variation taken from function one. Numbers represent sampling sessions 1 (□) – 4 weeks, 2 (□) – 8 weeks, 3 (□) – 12 weeks, 4 (□) – 16 weeks, 5 (□) – 20 weeks, 6 (□) – 24 weeks.

2.3.2 – Main effects of disturbance frequency

2.3.21 – Stage One - Mature Panels

In the mature communities the ANOVA showed that there were no significant effects of disturbance on any of the response variables during the first half of the experiment from weeks 4 to 12 ($P>0.05$). During the second half of the experiment, from week 16 onwards, disturbances always affected the total abundance of communities (16 weeks: $F_{6,119} = 5.04$, $P<0.001$; 20 weeks: $F_{6,119} = 7.96$, $P<0.001$; 24 weeks: $F_{6,119} = 7.67$, $P<0.001$). *Post hoc* analyses always placed these differences between communities never or rarely disturbed and those disturbed every second week during week 16 of the experiment. At weeks 20 and 24 this pattern remained significant but differences also occurred between communities disturbed every 4 and 6 weeks ($P<0.05$, Fig. 2.9). The species richness of communities was only significantly affected at week 24 as ($F_{6,119} = 4.84$, $P<0.001$: Fig. 2.10).

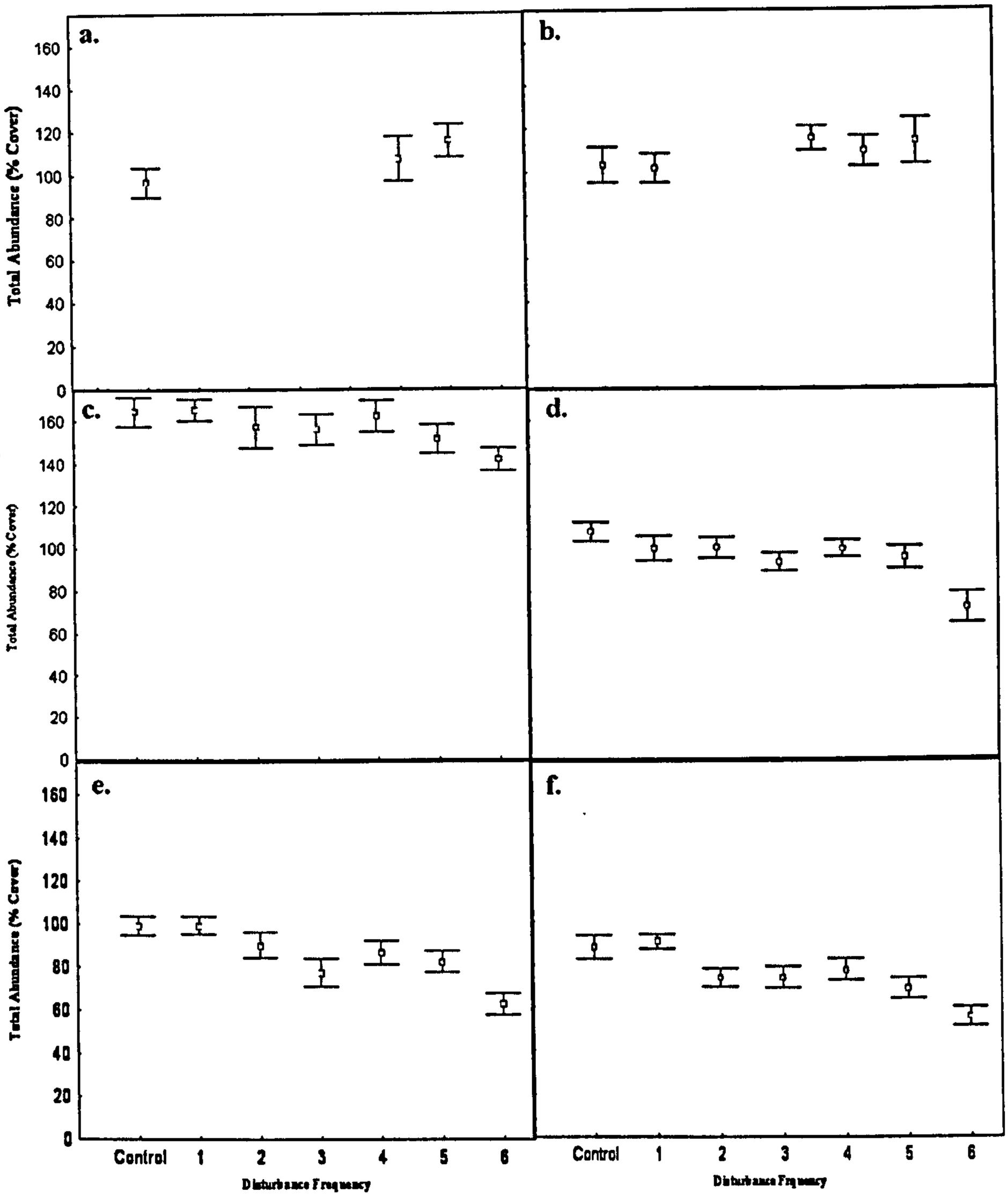


Figure 2.9 - Influence of disturbance frequency on the total abundance of mature communities at a. 4 weeks, b. 8 weeks, c. 12 weeks, d. 16 weeks e. 20 weeks and f. 24 weeks. Mean values at ambient nutrient availability, standard error around the mean are indicated by whisker bars. Disturbance frequency increases from a control of no disturbance to 6 – disturbed every 2nd week. Missing values in a. and b. indicate that no disturbance had occurred at this point in time.

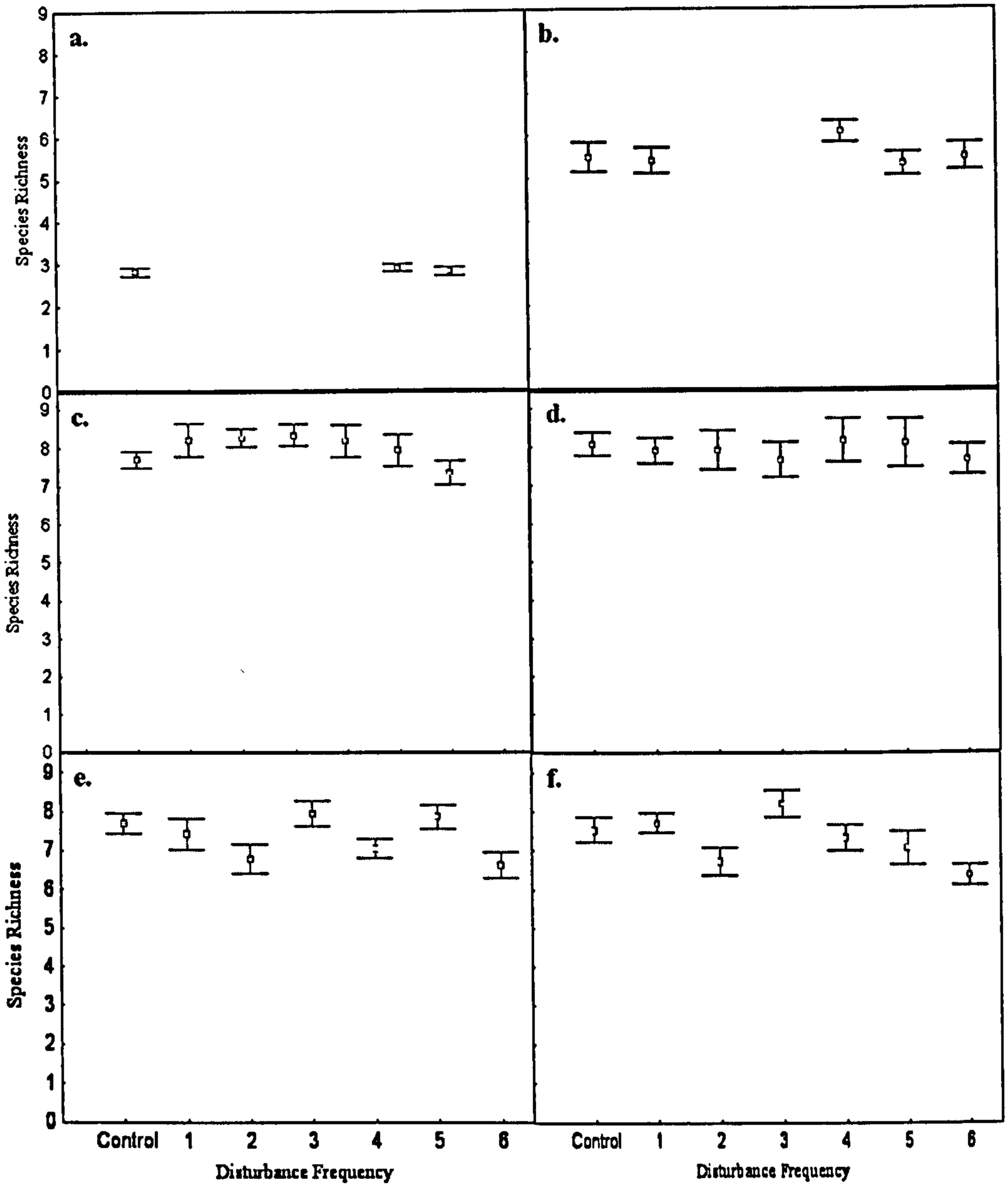
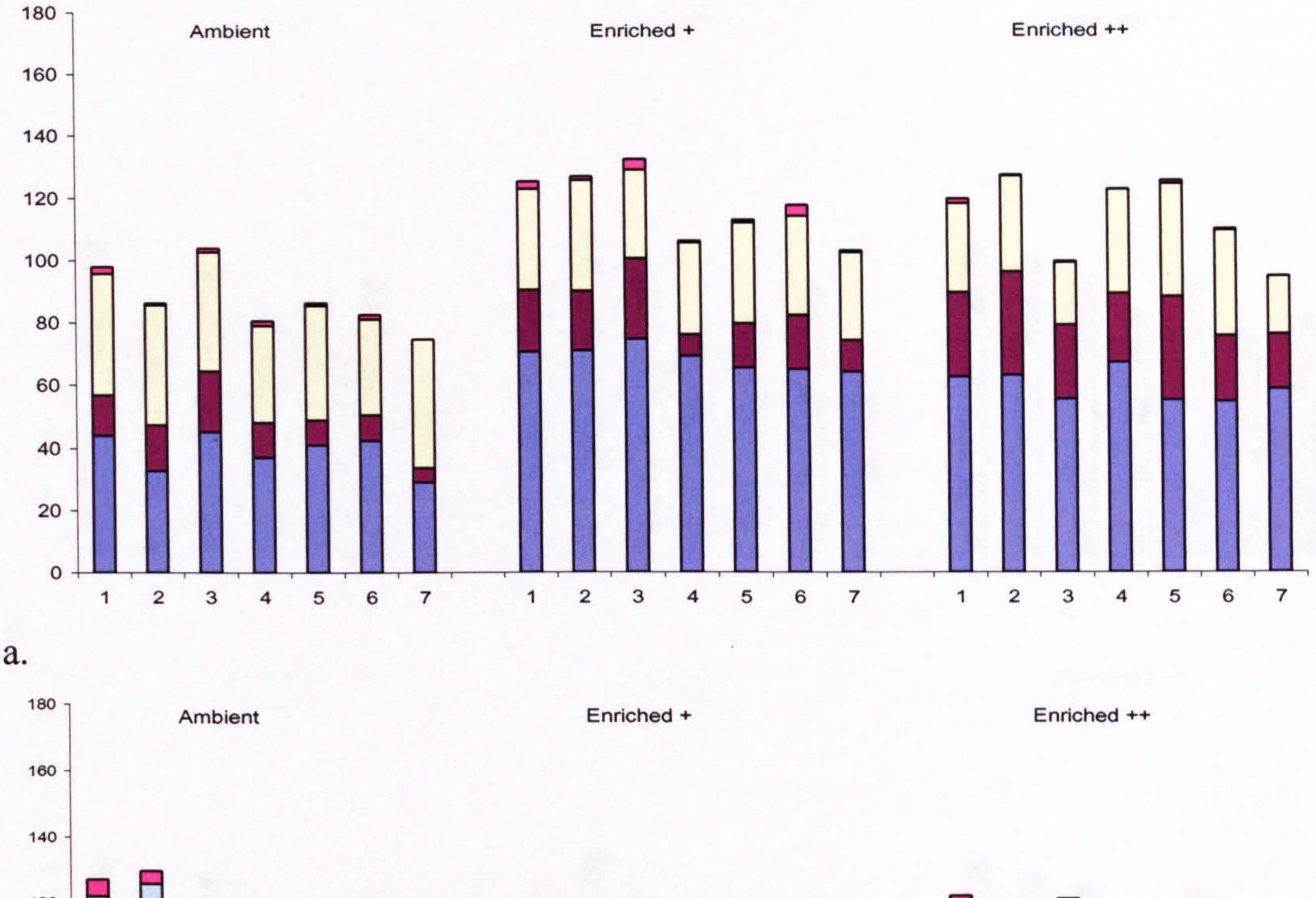


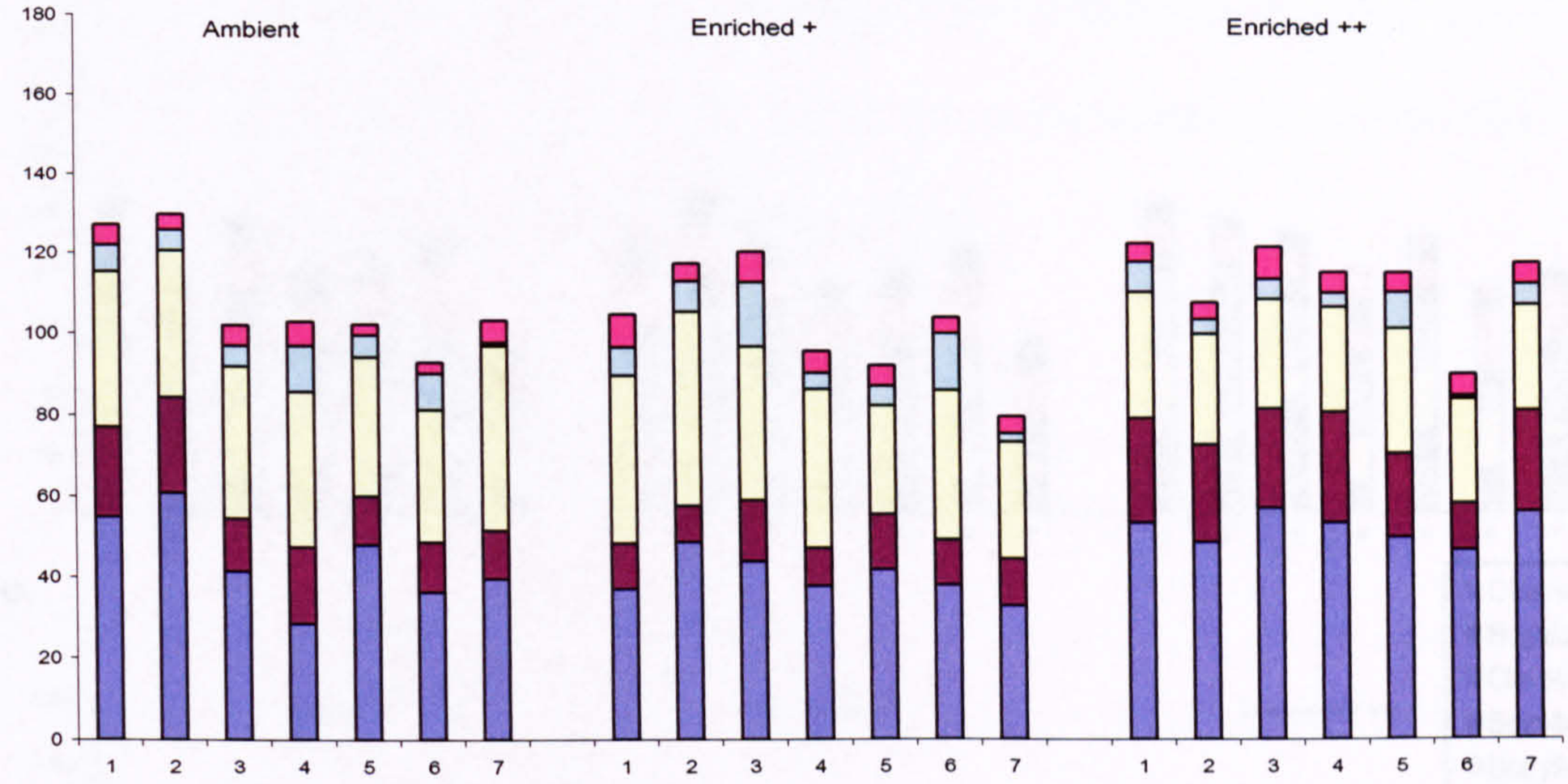
Figure 2.10 - Influence of disturbance frequency on the species richness of mature communities at a. 4 weeks, b. 8 weeks, c. 12 weeks, d. 16 weeks e. 20 weeks and f. 24 weeks. Mean values at ambient nutrient availability, standard error around the mean are indicated by whisker bars. Disturbance frequency increases from a control of no disturbance to 6 – disturbed every 2nd week. Missing values in a. and b. indicate that no disturbance had occurred at this point in time.

ANOSIM analysis showed that there were no significant differences between the species composition of the communities across all disturbance levels throughout the experiment. SIMPER analysis was then done to discover which species contributed the most to the communities.

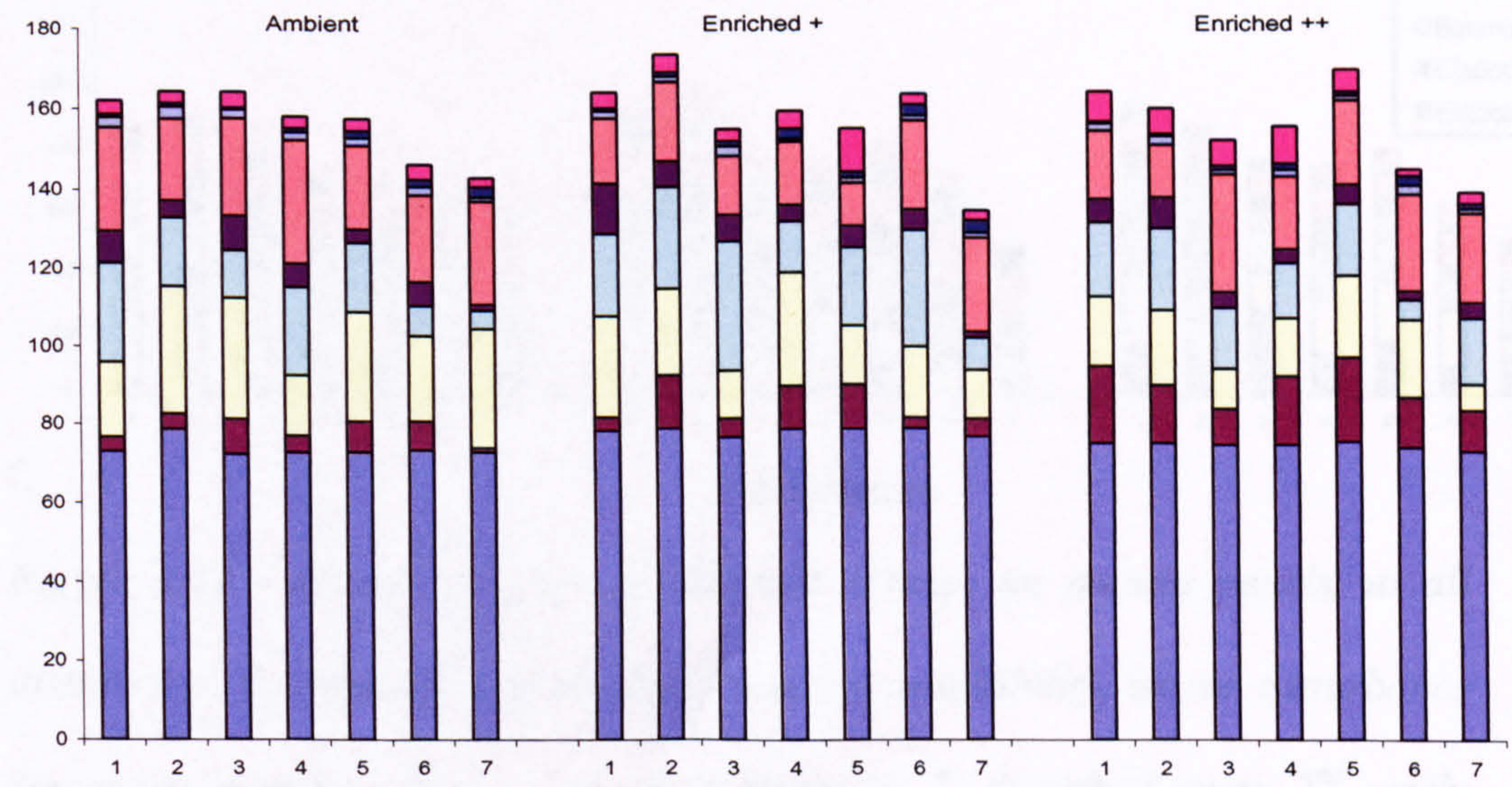
At 8 weeks the communities were comprised of *E. siliculosus, C. rupestris and B. crenatus* (approximately 42%, 10% and 70% respectively), across all disturbance frequencies. As the effects of disturbance frequency became more pronounced, solitary ascidians such as *A. aspersa* and *C. intestinalis* begin to replace the early communities. At 16 weeks *E. siliculosus* has almost completely disappeared and solitary and colonial ascidians (*B. leachi* and *B. schlosseri*) now make up approximately 60% of the community. Bryozoans such as *B. flabellata* have also increased and make up 10%. At 24 weeks the ascidians remain an important part of the community structure but algae have begun to increase in abundance, this is reflected across all disturbance frequencies (Fig. 2.11 a-f).



a.



b.



c.

Disturbance

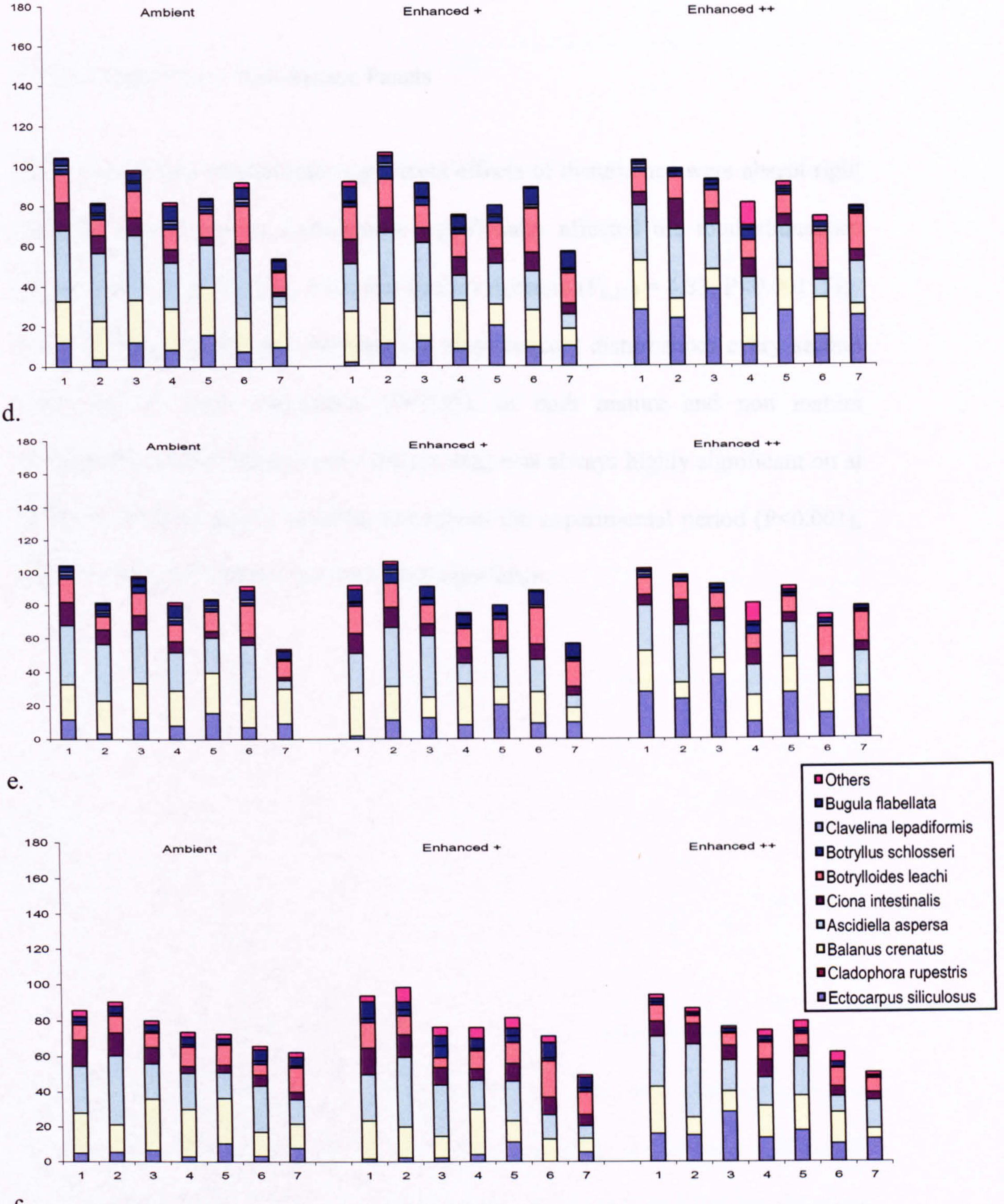


Figure 2.11 - Mean % cover of dominant species on mature panels, at all disturbance frequencies and levels of nutrient availability, where disturbance frequency increases from 1- no disturbance to 7- disturbed every 2nd week; Sampling sessions a – 01, b – 02, c – 03, d – 04, e – 05, f - 06.

2.3.22 – Stage Two – Non-Mature Panels

In the non mature communities significant effects of disturbance were absent right up until week 24 when disturbances significantly affected the total abundance ($F_{6,119} = 7.67$, $P<0.001$: Fig. 2.12) and species richness ($F_{6,119} = 4.83$, $P<0.001$: Fig. 2.13). Differences occurred between the very frequent disturbances every second week and all other frequencies ($P<0.05$). In both mature and non mature communities spatial heterogeneity (factor ring) was always highly significant on at least one of the response variables throughout the experimental period ($P<0.001$), except at week 24 where it was no longer significant.

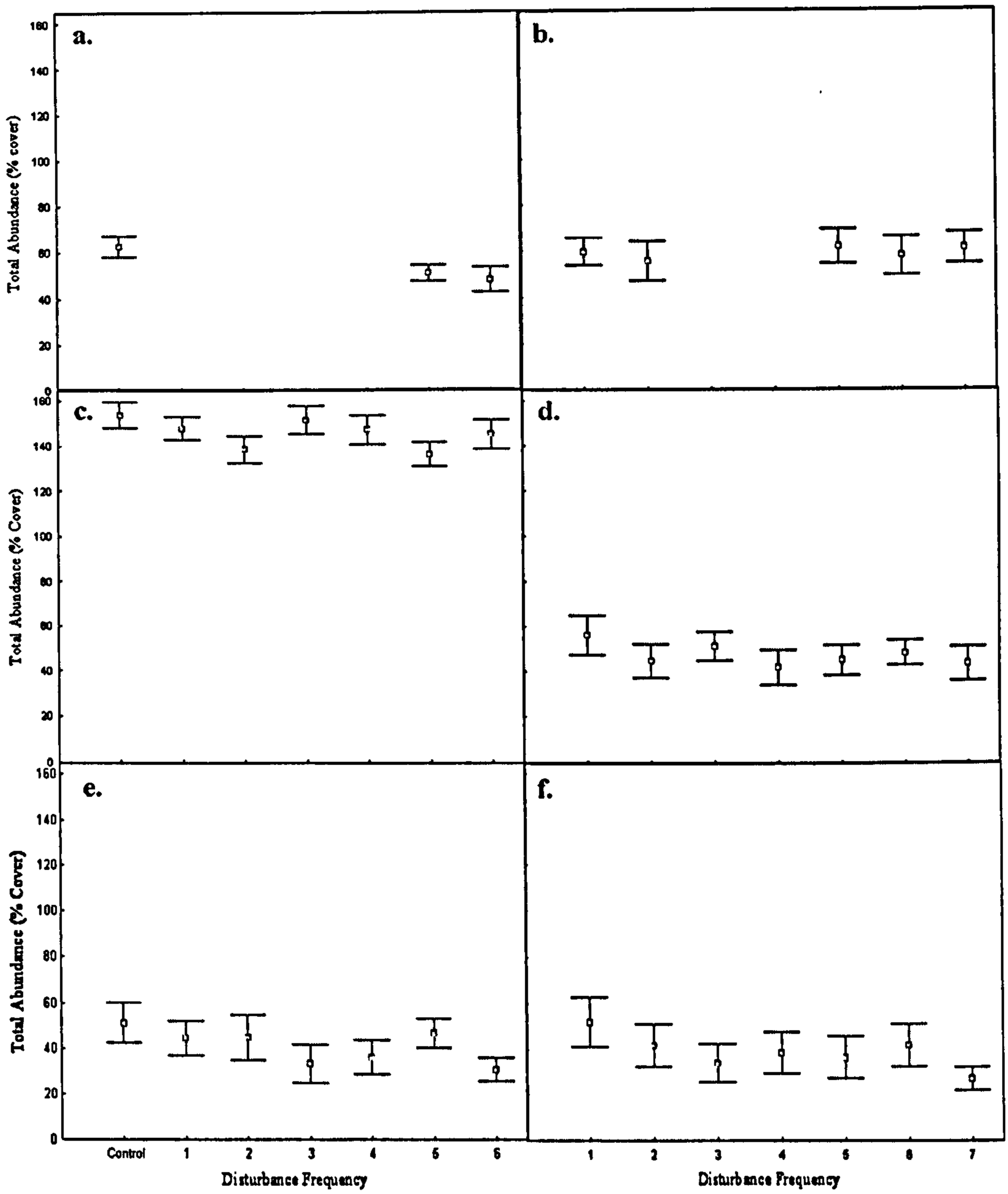


Figure 2.12 – Influence of disturbance frequency on the total abundance of non mature communities at a. 4 weeks, b. 8 weeks, c. 12 weeks, d. 16 weeks e. 20 weeks and f. 24 weeks. Mean values at ambient levels of nutrient availability, standard error around the mean are indicted in the whisker bars. Disturbance frequency increases from a control of no disturbance to 6 – disturbed every 2nd week. Missing values in a. and b. indicate that no disturbance had occurred at this point in time.

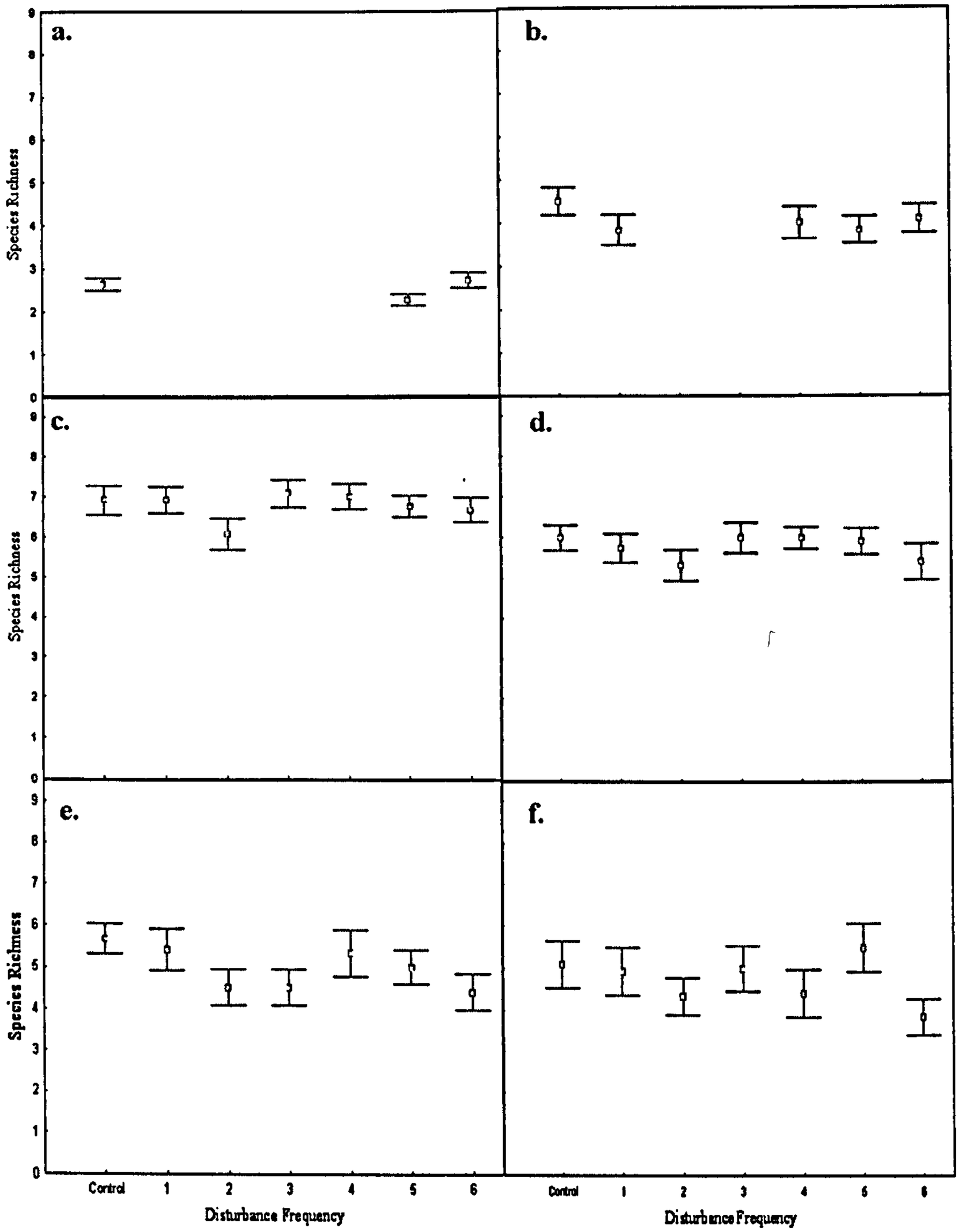
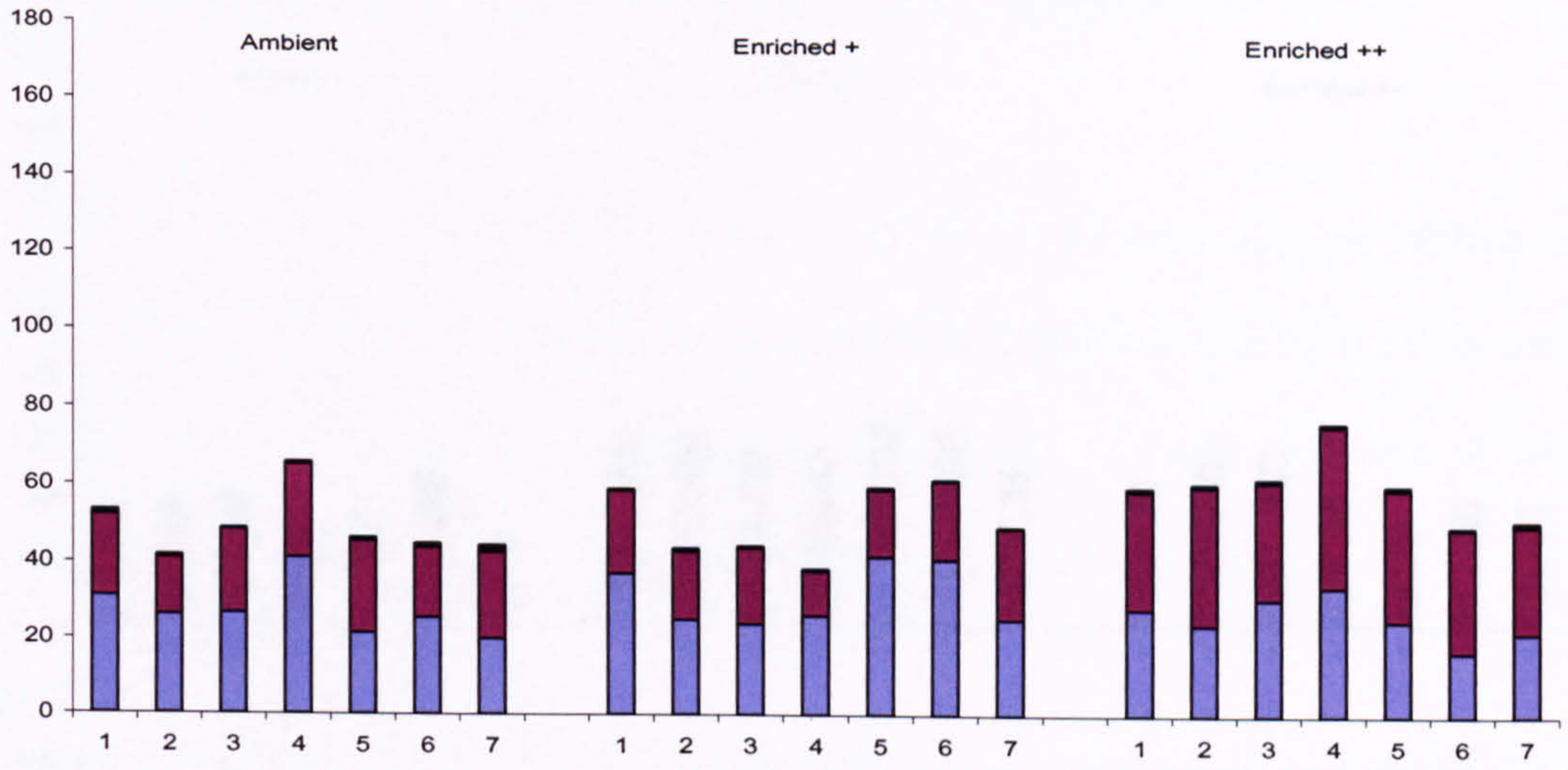


Figure 2.13 – Influence of disturbance frequency on the species richness of non mature communities at a. 4 weeks, b. 8 weeks, c. 12 weeks, d. 16 weeks e. 20 weeks and f. 24 weeks. Mean values at ambient levels of nutrient availability, standard error around the mean are indicted in the whisker bars. Disturbance frequency increases from a control of no disturbance to 6 – disturbed every 2nd week. Missing values in a. and b. indicate that no disturbance had occurred at this point in time.

ANOSIM analysis showed that there were some significant differences in the species composition at 24 weeks between disturbance frequencies every 12 and 8 weeks, (R= 0.352 P= 0.04). SIMPER analysis attributed these differences to contributions by *E. siliculosus, B. leachi* and *A. aspersa*.

After 8 weeks *E. siliculosus* and *C. rupestris* dominated the experimental communities comprising approximately 90% (SIMPER analysis) of the community. Other species were present in small numbers. At 12 weeks the cover of *C. rupestris* was greatly reduced and the numbers of other species dramatically increased. Ascidians such as *A. aspersa, B. leachi* and *B. schlosseri* and the bryozoan *B. flabellata* now contributed to 90% of the community. At 16 weeks *E. siliculosus* almost disappeared and total cover was reduced. At 24 weeks *E. siliculosus* began to recover though never re-establishing dominance and total species richness began to fall. Ascidians and bryozoans now dominated the community (Fig. 2.14).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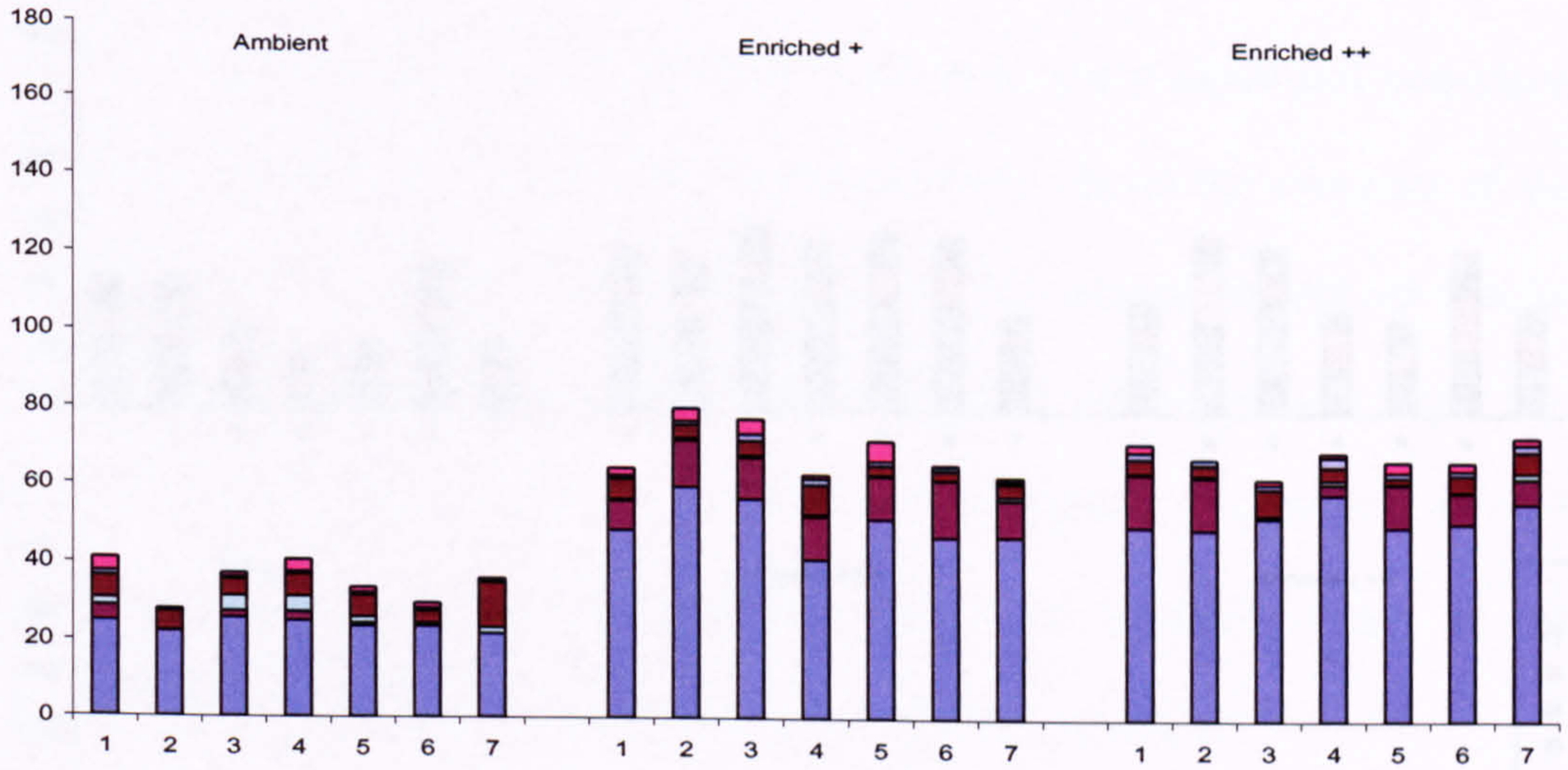
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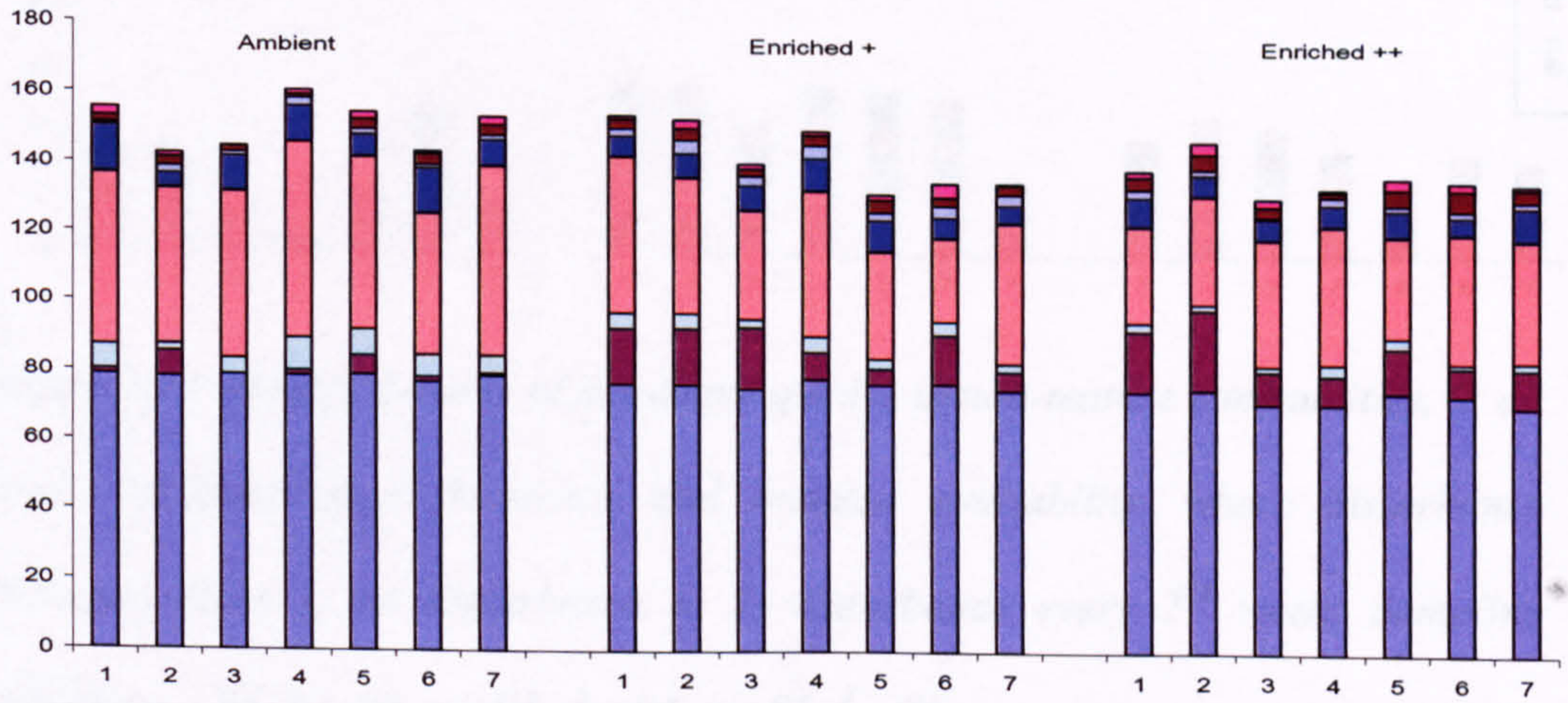
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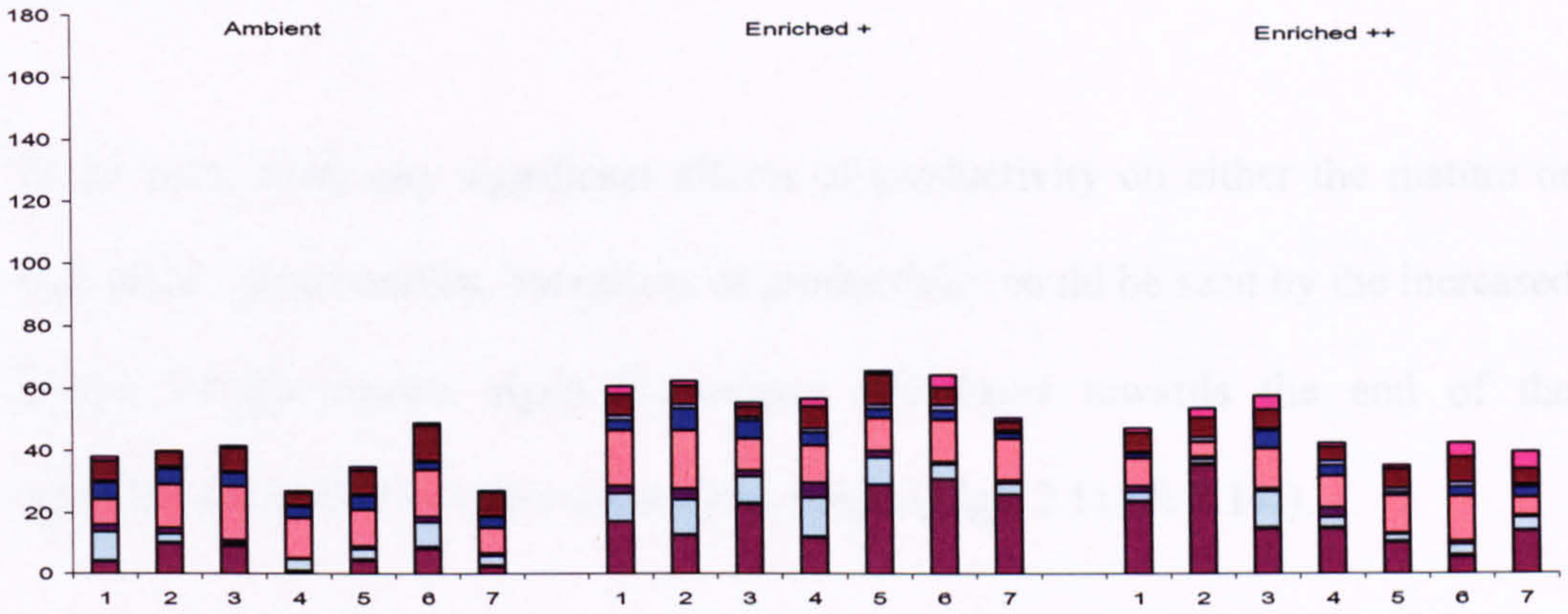

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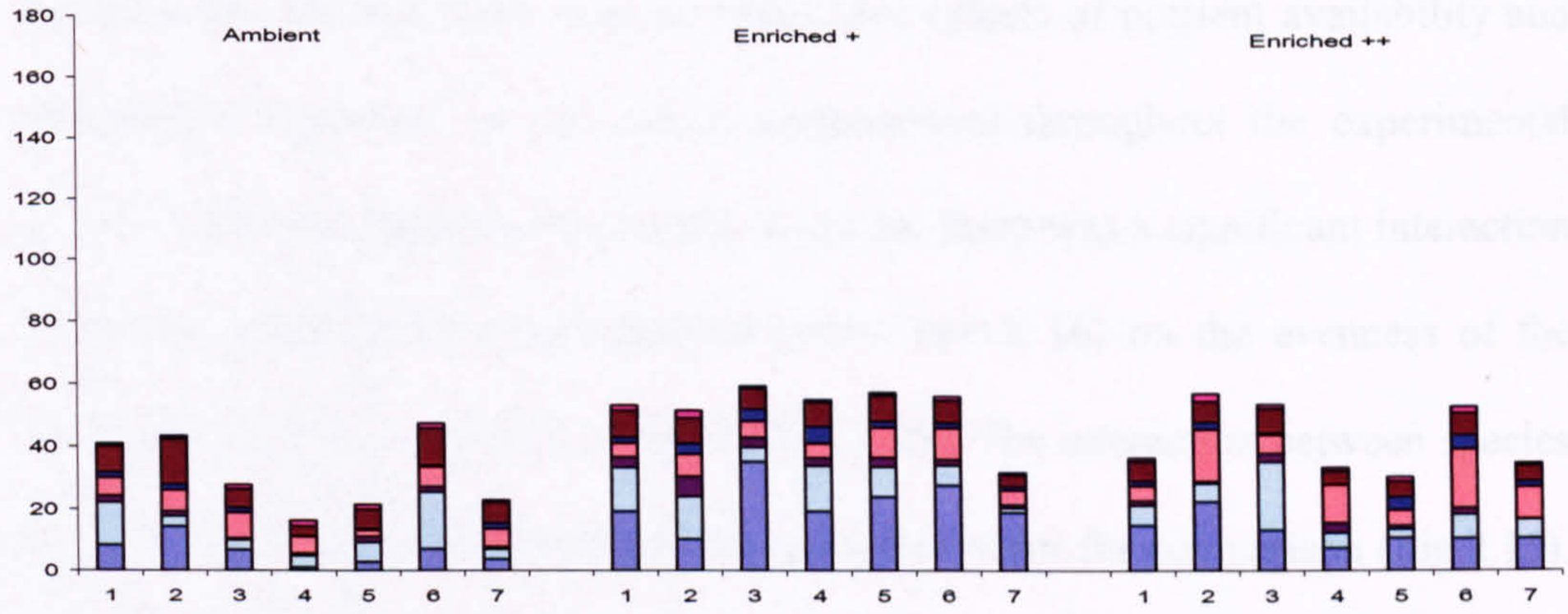
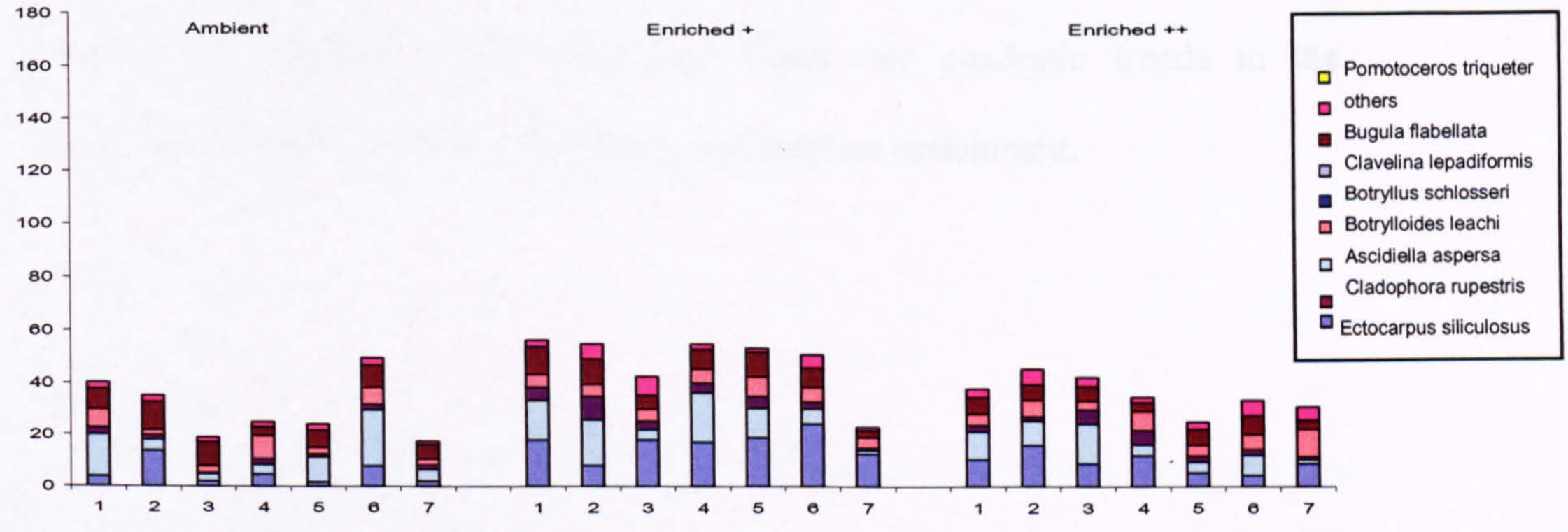


e.



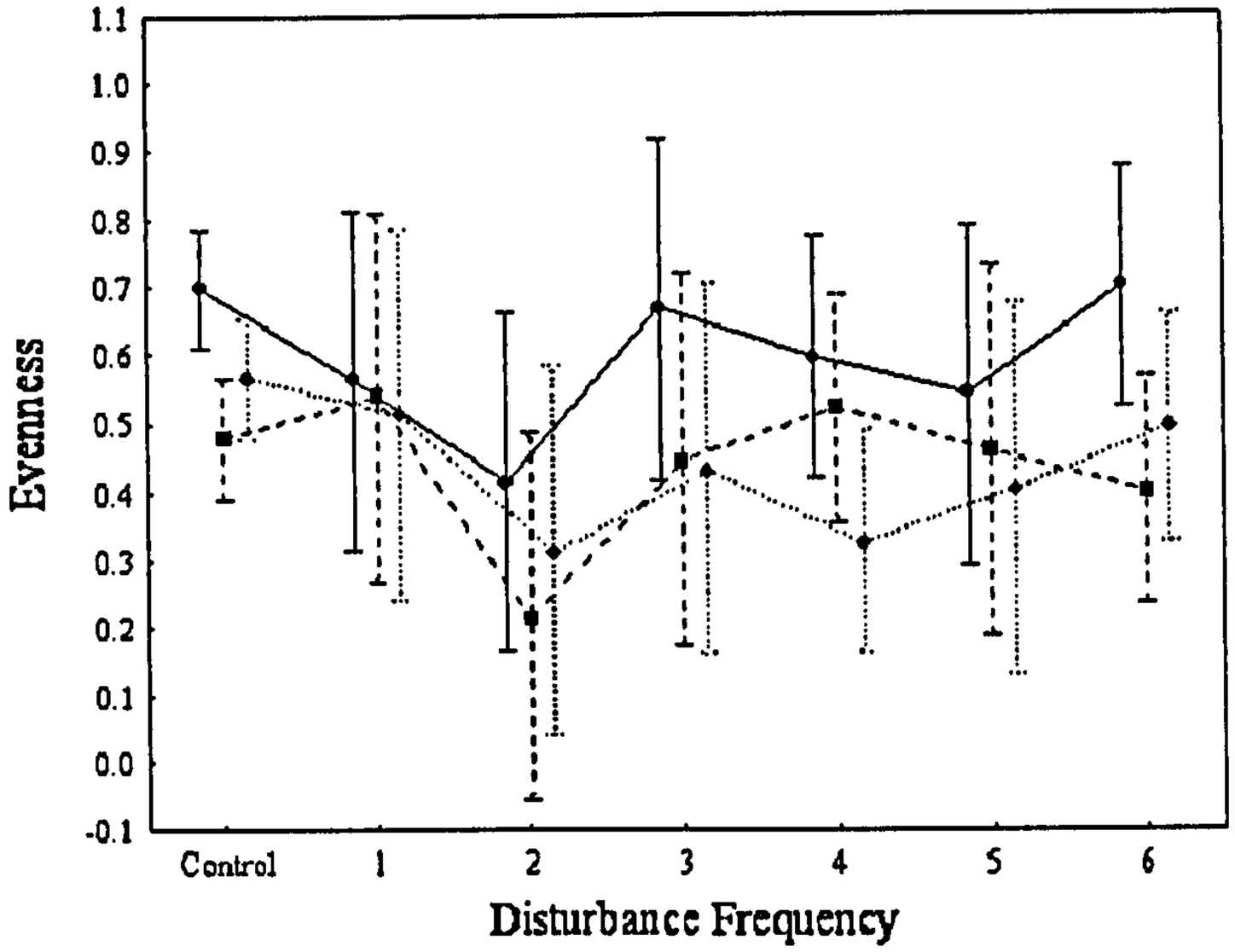
f.

Figure 2.14 - Mean % cover of dominant species in non-mature communities, at all levels of disturbance frequency and nutrient availability, where disturbance increases from 1- no disturbance to 7- disturbance every 2nd week; Sampling sessions a – 01, b – 02, c – 03, d – 04, e – 05, f – 06.

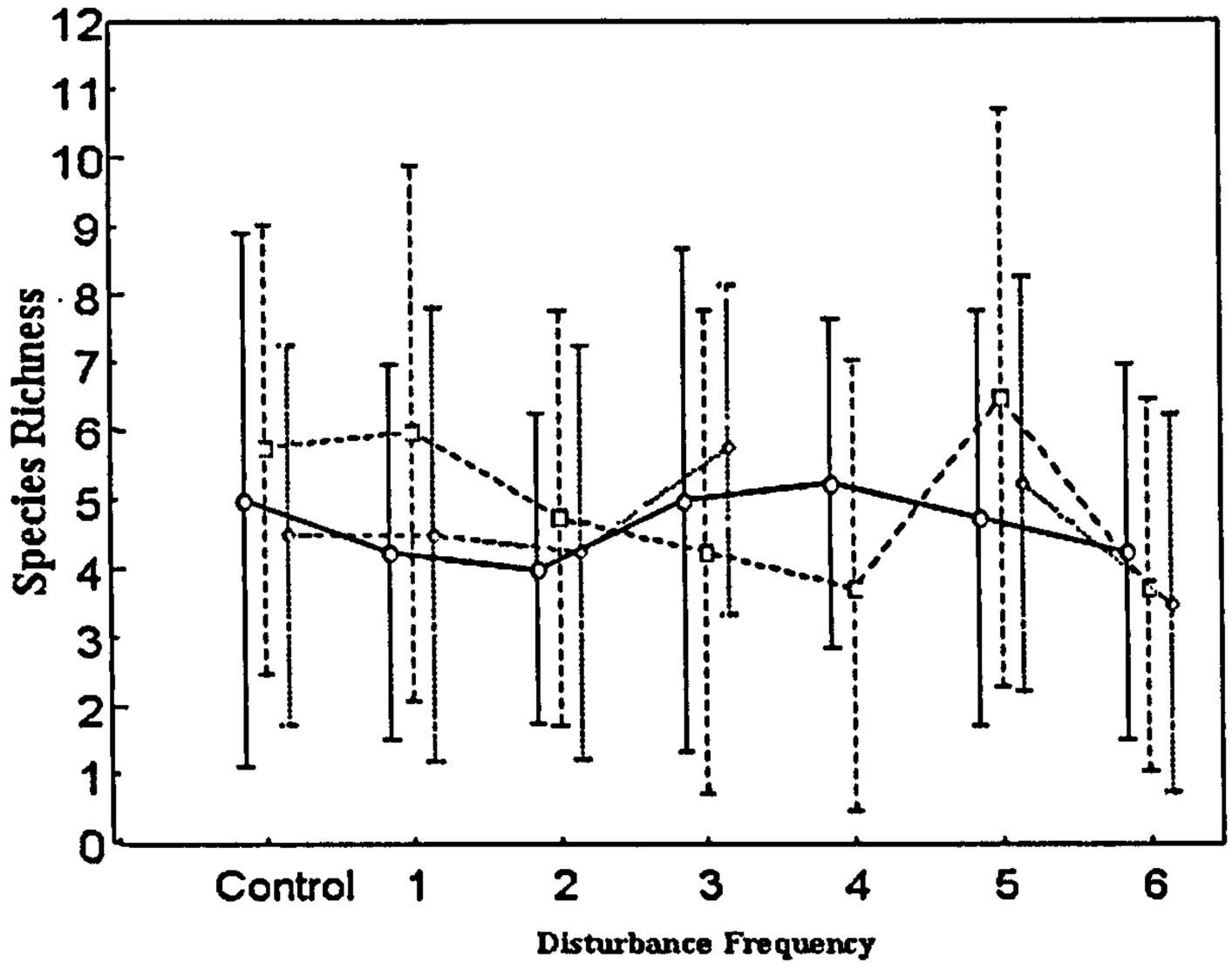
2.3.3 – Interactive Effects of Disturbance and Productivity

There were never any significant effects of productivity on either the mature or non-mature communities, but effects of productivity could be seen by the increased growth of the brown algae *Ectocarpus siliculosus* towards the end of the experimental period in both communities stages (Figs. 2.11f & 2.14f).

Analyses showed that there were no interactive effects of nutrient availability and disturbance frequency on the mature communities throughout the experimental period. In the non mature communities however, there was a significant interaction during the middle of the experimental period (week 16) on the evenness of the communities ($F_{12,119} = 8007.5$, $P<0.001$: Fig 2.15). The interaction between species richness is also shown for the same time period in order for comparison (Fig.2.15). This is when recruitment rates were probably at their highest. Despite this, *a priori* contrast tests detected neither significant linear nor quadratic trends in the interaction between disturbance frequency and nutrient enrichment.



a.



b.

Figure 2.15 – The interactive effects of disturbance frequency and nutrient availability on the a. evenness and b. species richness of non-mature communities at 16 weeks. Mean and standard error are shown at each level of nutrient enrichment (—Ambient, --- enriched, ····· Super-enriched). Disturbance frequency increases from a control of no disturbance to 6 – disturbed every 2nd week.

2.4 – Discussion

The aim of this study was to test the interaction between nutrient availability and disturbance frequency, as a test of the theoretical model proposed by Kondoh (2001). Kondoh proposed that the nutrient availability of a system would alter how the communities of that system are affected by a given disturbance frequency in respect to disturbance – diversity relationships (Connell 1978). He suggested that in communities where the classical unimodal pattern of species diversity along a gradient of disturbance was evident, the peak of this pattern would be shifted to higher disturbance frequencies with an increased availability of nutrients. A higher frequency of disturbance is therefore needed to maintain maximum diversity under increased levels of productivity (Kondoh 2001).

In order to achieve the primary aim of this study the effects of the disturbance frequencies that were applied to the communities were examined. Disturbances which resulted in a loss in biomass from a community (Grime 1977) affected the subtidal macrobenthic community on a temporal scale. In the non mature communities disturbance effects were only evident at the end of the experiment, whilst in the mature communities this could be seen from week 16 onwards, due to the more frequent disturbances creating a reduction in the total abundance of the community. However, since the relative abundance of the dominant species *E. siliculosus* remained constant on the disturbed panels it supports the idea that it was the subordinate species in the community that were unable to cope with the

repeated disturbances. Although *E. siliculosus* is typically an opportunistic species which would normally be out competed in long lived communities, the frequent disturbances applied in this experiment allowed it to continually re-colonise the cleared patches and establish and maintain dominance (Warwick & Ruswahyuni 1987, Beukema 1988, Weston 1990).

The total abundance of the non mature communities was affected by the disturbances; it was reduced with an increase in disturbance frequency following the same patterns as those shown by the mature communities. However, the younger communities were not affected by disturbance frequency in any other parameters, such as species richness. Because the relative proportion of the area of covered by the non-mature communities was always less than that covered by the mature panels, the probability of some of the species being impacted is accordingly less. We therefore suggest that communities at an older successional stage, which are heavily dominated by one or two species, are less stable than those at younger successional stages where a number of species are still competing for dominance and have greater colonising abilities (cf. Sutherland & Karlson 1977). Older communities will suffer more damage for a given level of disturbance (Sousa 1980).

The composition of species between the communities at the different stages of succession was significantly different from one another throughout the experimental period. These differences could be due to the temporal pattern of recruitment within the system over the maturing phase and subsequent

experimental phase. For example the barnacle, *Balanus crenatus* (Brugiere, 1789), which contributed largely to the observed differences between the two successional stages, was present only in mature communities. This suggests that the spawning period of this species occurred only in the maturing phase of the experiment, and that this could have contributed largely to one of the reasons the two communities never became similar (Cowie et al. 2000, Huxham et al. 2000). In the mature communities barnacles could also have provided a secondary substratum and habitat heterogeneity, which was more attractive to the settlement of epibionts, than the bare space associated with the non-mature communities.

Interestingly the effect of spatial heterogeneity was nearly always highly significant, suggesting a large amount of spatial heterogeneity within the site, and it was only when these effects were less prominent that the effects of disturbances became evident. This could mean that the effects of space were overshadowing the effects of disturbance and heeds caution in future experimental designs of this nature as well as the interpretation of the results.

Interactive effects between nutrient availability and disturbance frequency were only observed at week 16 on the evenness of the non-mature communities. Despite this, the interaction appears to show the opposite effects to those predicted by Kondoh (2001). It seems that at ambient levels of productivity maximum evenness, in this case, is found at very low and very high disturbance frequencies. A similar pattern to this can be seen in the nutrient availability, at the very low and very high disturbance frequencies it appears that evenness peaks at ambient and super

enriched levels creating an inverted polynomial pattern. At the more intermediate disturbance frequencies this relationship becomes linear. However, at present we are unable to fully interpret this relationship due to the lack of significant *a priori* contrasts, likely caused by the large spread of the data. The appearance of this interaction at 16 weeks matches the temporal pattern in recruitment, which peaked at mid summer.

Due to these findings our data do not support the IDH or the DEM in the system that we investigated. This is by no means a definitive answer and is only applicable to the treatments that we applied. It seems clear that disturbances do alter community compositions, and it also seems clear that there is an interactive effect between nutrient availability and disturbance frequency, but there are no effects of disturbance on species diversity or richness. Although it may be considered by others to be a short experiment in terms of community stability (Sutherland & Karlson 1977), the site, as well as being very sheltered with infrequent disturbances, has been previously shown to have a low temporal variability (Prendergast 2007), and studies on natural communities elsewhere show that using similar measures of community structure have indicated a similar level of stability (Kay & Butler 1983). These results may therefore be more widely applicable than previously thought. The use of larger or smaller settlement panels would not have changed the results due to all species being present in the communities (Bakus 1988). However if the surface of the panel was different, for example a change in the roughness, it is likely that the results would have altered (Walters & Wethey 1996).

In eight identical experiments, conducted as part pf the GAME programme, at four study sites across the Northern hemisphere there was direct support for the IDH in Sweden but no interactive effects with nutrient enrichment (Svensson et al. 2007). Similar results were found in Italy as those reported herein with transient interactions between disturbance frequency and nutrient enrichment (Spindler et al., personnel communications), whilst there was no support for either the IDH or Kondoh's model in Madeira (Clode et al, personnel communications), or Japan (Miethe et al. personnel communications). In eight identical experiments conducted at four study sites across the Southern hemisphere the unimodal relationship between disturbance and diversity was observed in the fouling communities on the N. Central Chilean coast (Valdivia et al. 2005). Interactive effects between disturbance and productivity as suggested by (Kondoh 2001) were only observed in Brazil (Jara et al. 2006).

Thus, the use of the model predicted by (Kondoh 2001) and the IDH (Connell 1978) as tools to predict diversity patterns and therefore management plans in temperate shallow subtidal systems needs to be carefully re-examined. In order to find the unimodal curve as predicted by these models a certain number of factors need to be present. These factors such as competitive exclusion and recruitment remain elusive and difficult to quantify under experimental field conditions, resulting in circumstances where models such as these are difficult to empirically test. It is clear that more experimental work in a range of natural ecosystems is

needed in order to refine the models in question so that they may be used to effectively predict patterns of biodiversity.

The effects of these two factors were however tested in isolation of the entire range of factors that are known to control species diversity. With increasing recognition that natural systems are highly variable it is acknowledged that the results presented here could be very different if they were inflicted at different periods of time, intensity, frequencies or if disturbance events were more variable.

Chapter Three: The temporal variability of disturbance regimes: Is this important for the diversity and community composition of benthic subtidal assemblages?

3.1 - Introduction

As a result of external processes, such as disturbances, natural communities are characteristically variable, fluctuating in both space and time (Landres et al. 1999, Fraschetti et al. 2005) and an understanding of this variability is essential for the management of species assemblages within ecosystems (Wu & Luocks 1995, Benedetti-Cecchi et al. 2000). It is crucial to understand how these processes influenced ecological systems in the past and how they might affect communities in the present and in the future with a view to managing systems and sustaining biodiversity (Landres *et al.* 1999). Understanding natural variability draws on a number of disciplines but it is disturbance ecology which provides an understanding about both the spatial and temporal dynamics of communities and how different species assemblages respond to these driving forces over temporal periods (Landres *et al.* 1999).

Biotic and abiotic disturbances are widely accepted as playing a critical role in influencing the patterns of distribution, abundance and diversity of species (Shea et al, 2004). A disturbance can be defined as 'a temporally discrete event which abruptly kills or displaces individuals, or that directly results in a loss in biomass from a system' (Grime, 1977). A disturbance therefore not only increases mortality within a community, but it may also change the availability of resources creating opportunities for different species, that would otherwise be outcompeted, to exploit (Connell, 1978; Roxburgh, 2004).

The response of a species to a disturbance is a trade off between its susceptibility/resistance to a disturbance and its ability to utilise newly opened resources, e.g. space for colonisation, either by in-growth from surrounding areas or the recruitment of propagules (Connell 1978). If a disturbance is repeated then this can be considered to be a regime, i.e. a sequence of events at regular or variable intervals. Temporal variability in a disturbance regime can be vital in affecting the outcome of this trade off. For example, highly variable disturbance regimes are expected to be more concentrated with a clustering of disturbance events and greater periods of recovery. This could have severe implications for species with very short recruitment periods that coincide with the clustered disturbances, they are potentially excluded from the assemblage, and the same could be true for species with specific growth rates, thereby increasing competitive exclusion. When disturbances are less variable, i.e. spaced more evenly over time, we could expect a reduction in competitive exclusion allowing the existence of both life strategies commonly present in benthic assemblages, i.e. opportunists and strong competitors (Benedetti-Cecchi 2003).

The majority of studies in experimental ecology have focussed on the variance, and more specifically the mean, in the response of a community to a driving force, e.g. a disturbance, and have largely ignored any of the variance inherent within this force. Therefore, little is known about the consequences of changing the variance in a driving force (e.g. a disturbance regime) over explicit spatial or temporal scales. Disturbance regimes are thought to become more variable with increasing global

change (Smith & Buddermeier 1992, Benedetti-Cecchi 2003). However, theoretical models suggest that the spatial and temporal variability of disturbance regimes are important and that they actually increase species diversity (Abugov 1982, Benedetti-Cecchi 2003). These aspects have been largely under explored in natural systems (Navarrete 1996). The few studies that have been done in this area have validated this concept, as well as suggested that variability may also influence patch dynamics (Butler 1989, Collins 2000).

Macro benthic assemblages were used in this study because they are short lived, they are therefore suitable to experimental manipulation conducted on relatively short time scales compared to some other systems (Dayton 1971, Sousa 1979). Sessile benthic assemblages were also chosen because they mostly lack interspecific trophic interactions (Wootton 1998), for example they do not prey on one another (cf. Boero et al. 2005), space is a limiting resource (Connell 1978) and two possible methods of colonisation occur either from the water column, in the form of larvae, or as lateral growth from surrounding species (Underwood & Chapman 1996, Sousa 2000). In this study we investigate the effects of a temporally variable disturbance regime (i.e. the distribution of disturbance events over time) and the specific timing of disturbance events within each of these regimes (i.e. its sequence), on the diversity of marine macro benthic assemblages on the North East coast of England.

3.2 - Materials and Methods

3.2.1 - Site Description

This experiment was carried out from March 2005 until October 2005 at two sites on the North East coast of England. Two sites were used to provide a contrast encompassing the extreme range of biotopes on the North East coast. It was logistically impossible to include more sites to provide a formal within-region spatial analysis. Each site is therefore considered as a separate experiment and analysed separately, but the informal comparisons between the two experiments are still very informative. The first site: Hartlepool Marina is a non-tidal, fully enclosed marina with access through a lock system (for a full site description and map of marina see section 2.2.1). The second site: Sunderland marina (54° 55' 05.47'' N, 1° 22' 02.10'' W; Fig. 3.1) is fully marine with salinity always >30 PSU although it is located at the mouth of the River Wear. Hartlepool marina has a fouling assemblage dominated by the solitary ascidians *Ciona intestinalis* and *Ascidiella aspersa*, and the erect growing bryozoan *Bugula flabellata*. Sunderland marina has a benthic assemblage consisting of green and brown seaweeds such as *Fucus* spp. and *Ectocarpus siliculosus*, barnacles, *Balanus crenatus* and tube worms, *Pomatoceros triqueter*. Recruitment occurs throughout the summer in both marinas.

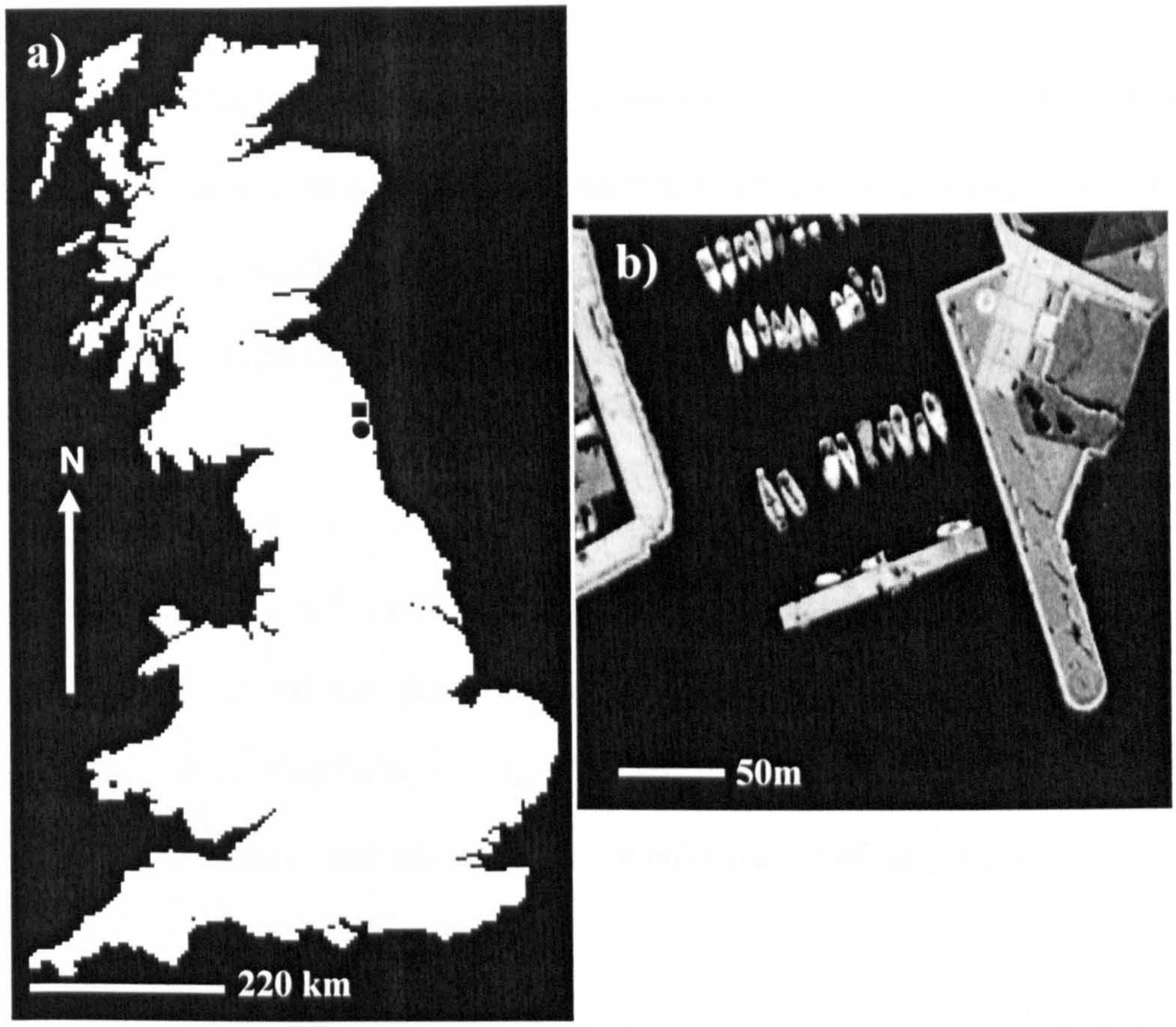


Figure 3.1 – Map of Great Britain (a) showing the location of Hartlepool marina (black dot) and Sunderland marina (black square), and b) a map of Sunderland marina.

3.2.2 - Experimental Approach

Roughened PVC panels were used as artificial settlement substrata and were prepared according to section 2.2.2. Settlement panels were arranged in a single row on PVC strips (205 x 25 x 0.3 cm). Panels were fixed reversibly to the strips with cable ties (100 x 2.5 mm) to allow the return of panels after sampling.

The experiment consisted of a two-factor nested design with temporal variability of disturbance as a fixed factor, and sequence of disturbance events over time as a nested factor. All panels were submerged at a depth of 50 cm in March 2005, at the two study sites. They were left here for two months before the beginning of the experimental manipulation to allow natural colonisation of the panels.

3.2.3 - Disturbance Regime

The disturbance treatment applied to the communities was the same as that used in Chapter 2 and a detailed description of this can be found in section 2.2.4. Temporal variation in disturbance was quantified by the standard deviation of the interval between disturbance events from the mean interval of 15 days. The frequency of disturbance events totalled 10 through out the experimental period of 150 days and treatments included a control of no disturbances (Control) and 3 levels of temporal variation: Constant variation (Constant; every 15 days), low variation (Low) and high variation (High), each level of variation was calculated using a standard deviation around the constant variance level and produced disturbance regimes with

at least 5 days between each disturbance event (Fig. 3.2). Within the low and high levels of temporal variation 3 different sequences of disturbance events were nested (Fig. 3.2). To avoid confounding the mean effect size with temporal variability in the disturbance regime both the intensity (20% of the panel area) and the frequency (10 events) were maintained constant in the experimental design. Moreover the time since the last disturbance before sampling the communities was kept constant (15 days, Fig. 3.2) for all treatment levels (Benedetti-Cecchi 2003). For each treatment 5 replicate panels were used, giving a total of 60 panels per experiment.

3.2.4 - Sampling

Each panel was photographed at the beginning of the treatment phase and then twice more at 75 days and at 150 days (Cannon G3 Powershot, 4 x 10^6 pixels). Pictures were downloaded and percentage cover of species was estimated in the same way as described in section 2.2.5. After 150 days the dry weight of the communities were taken and this was used as an estimate of the biomass for each community.

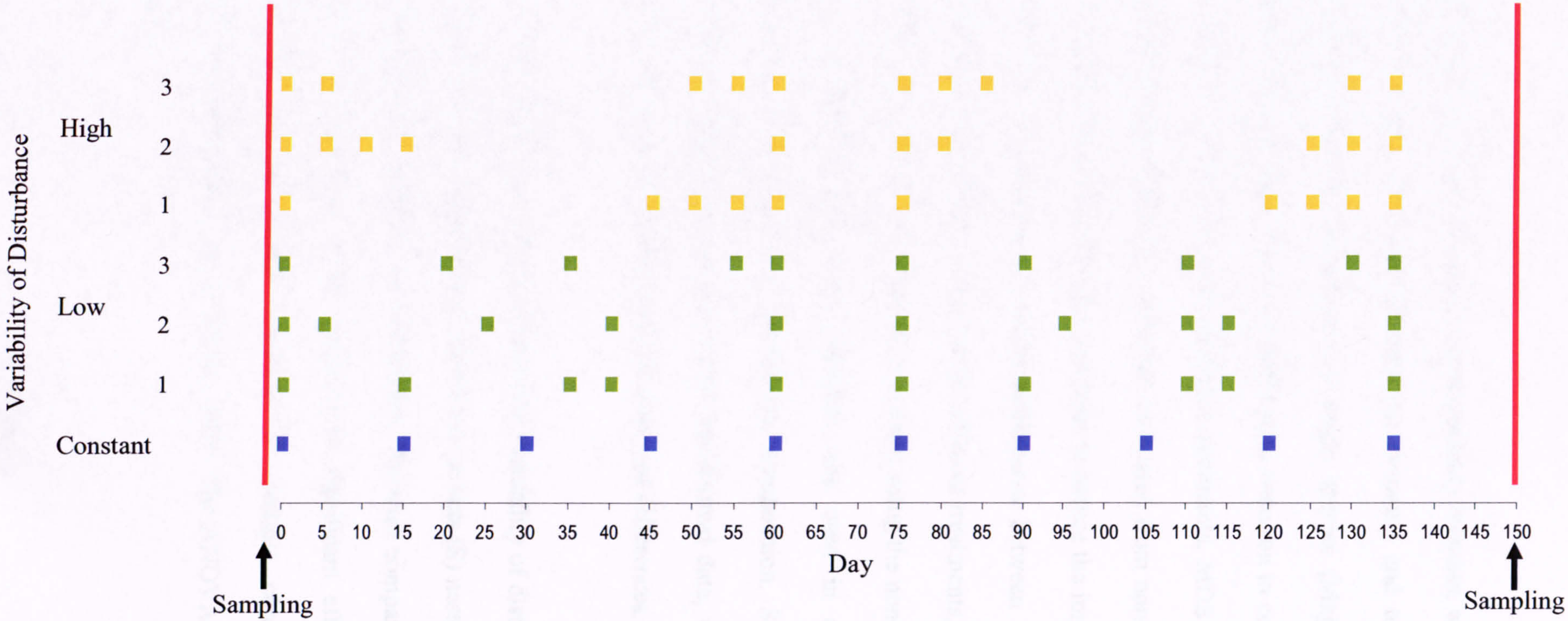


Figure 3.2 – Diagrammatic representation of variability of disturbance regimes over the experimental period of 150 days. Blue squares represent constant variability, while green squares represent low variability with its 3 sequences and yellow represents high variability with its 3 sequences. Arrows represents time when sampling was done and squares represent disturbance events.

3.2.5 - Data Analysis

Dry weight was used as a proxy for community biomass, while species diversity (Shannon index, H'), species richness, evenness and total abundance were calculated from the abundances of single species (Magurran 1988). Multi-dimensional scaling ordination (MDS) plots were run to compare differences in community composition under different treatments. MDS plots were based on the Bray Curtis similarity coefficient calculated from non-standardised, square root transformed data, the latter was done to reduce the importance of abundant relative to rare species. To detect differences between the compositions of community assemblages experiencing different treatments, a one way Analysis of Similarity (hereafter ANOSIM) was done; using the non-standardised, square root transformed data. This approach was used in order to provide a conservative comparison of assemblage composition. Similarity percentage analysis (SIMPER), using square root transformed data, was used to identify which species contributed most to the observed differences.

To test for significant effects of temporal variability of disturbance (V), as well as the effects of the sequence of disturbance events (S) nested within this factor, a mixed model ANOVA was undertaken. Pairwise comparisons with *post hoc* tests were performed in the presence of significant effects: t-tests on the estimated marginal means adjusted for multiple comparisons with the Bonferroni procedure (Day & Quinn 1989). The ANOVA followed the linear model;

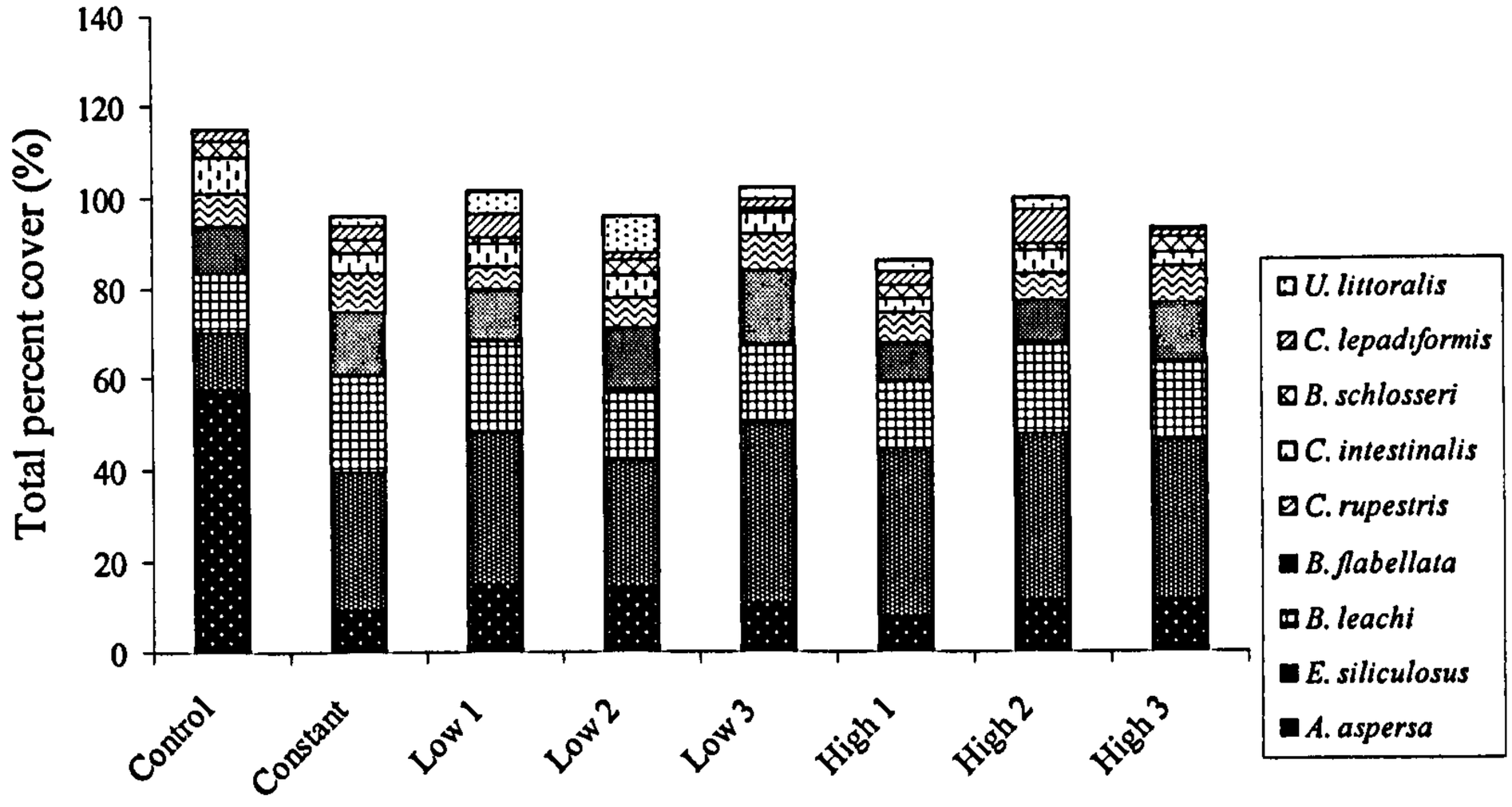
$$X_{ijkl} = \mu + V_i + S(V)_{j(i)} + B_k + e_{ijkl}$$

Where X_{ijkl} represents the response of a community *l* that is characterised by variability of disturbance *i*, the sequence of disturbance events *j* and is located on block *k*. μ is the mean of the response variable X. e represents the error. Variability of disturbance (V), Sequence of disturbance events (S) and Block (B), if they exist represent the effects of the treatments (Underwood 1997).

3.3 – Results

The sessile communities of the two experimental sites differed markedly in their species richness as well as the relative abundances of common species. A total of 14 species comprised the benthic community in Hartlepool whereas only 3 species were present in Sunderland (Fig. 3.3). In natural communities similarity percentage analysis (SIMPER) showed that *Ascidiella aspersa* (O F Müller, 1776) dominated in Hartlepool marina, with an average abundance of 58 % in the fouling community, however in Sunderland marina *Ectocarpus siliculosus* ((Dillwyn) Lyngbye, 1819) was the dominant species, with an average abundance of 89 % (Fig. 3.3). Multi-dimensional scaling (MDS) ordination showed that there was a difference between control (undisturbed) and disturbed communities in both Hartlepool and Sunderland marina (Fig. 3.4). Although the stress value for both study sites are considered high (0.2) and intermediate (0.11), ANOSIM validated the MDS ordination by showing that each level of variability of disturbance showed some significant dissimilarities from the control (Table 3.1).

a.



b.

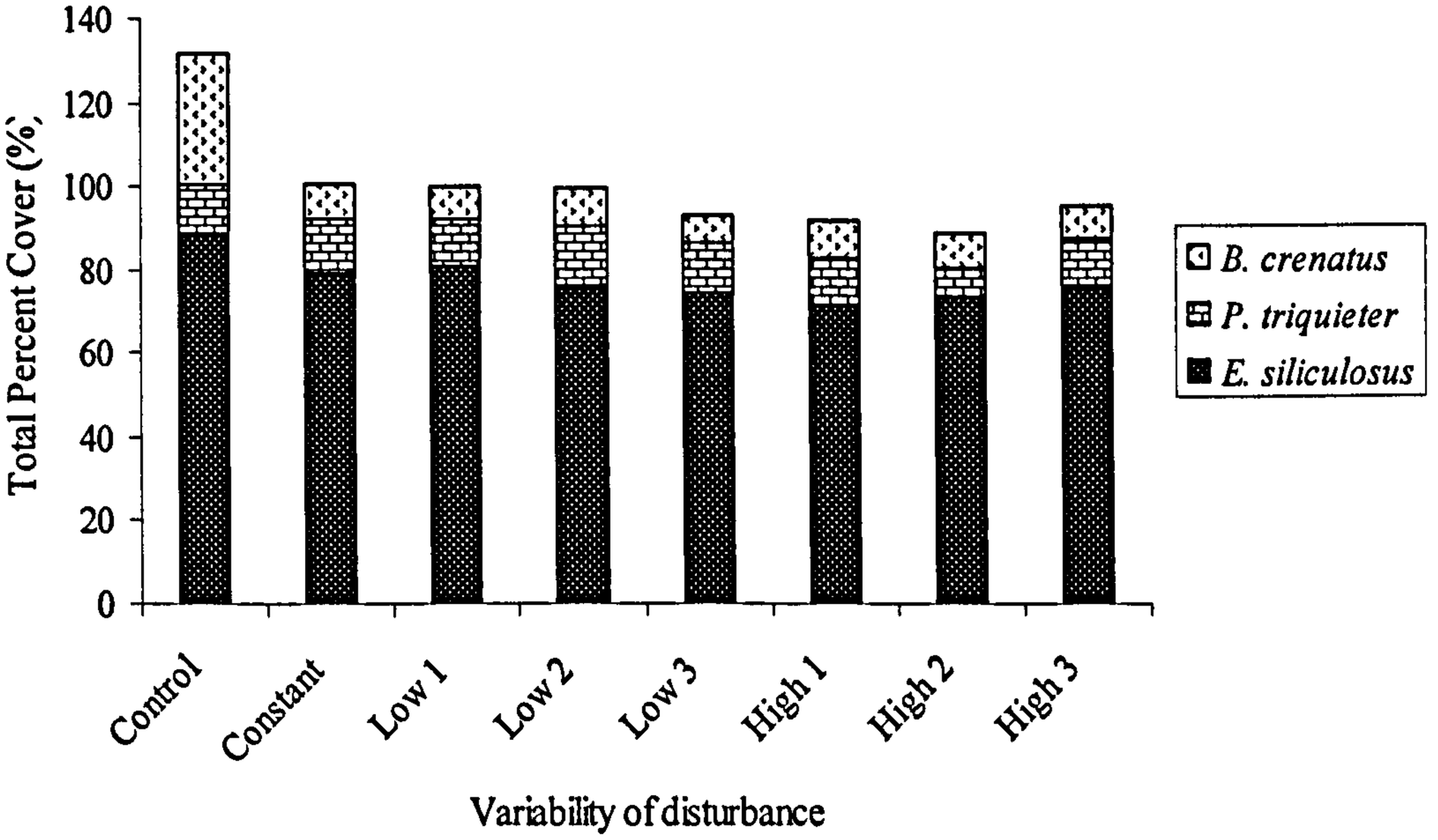


Figure 3.3 - Total percentage cover of species comprising 90 % of the community (based on SIMPER analysis) in a) Hartlepool marina and b) Sunderland marina, under different treatment levels. The numbers 1-3 represent the intrinsic sequence of disturbance events within each variability regime.

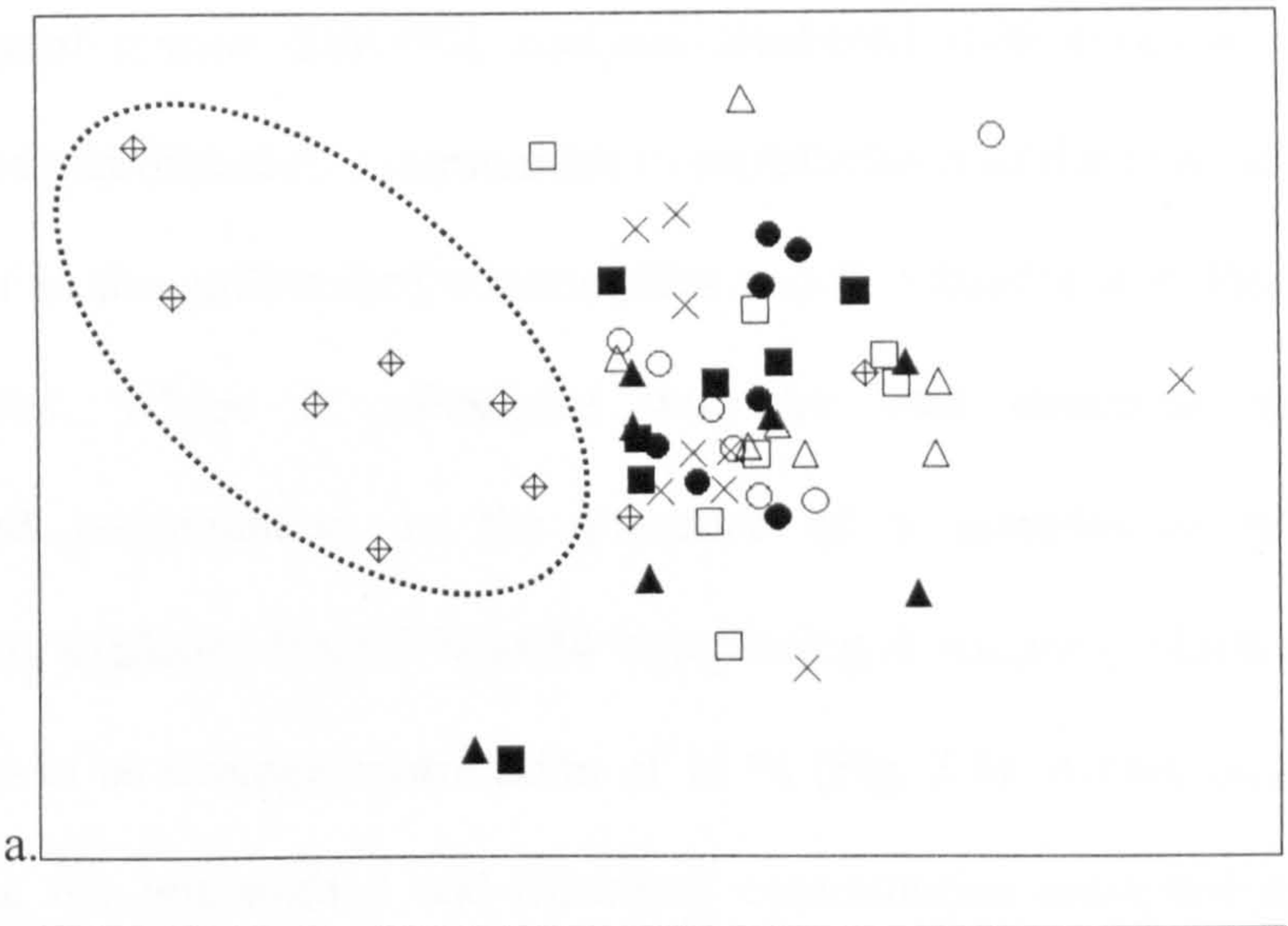


Figure 3.4 – Multi-dimensional scaling ordination of communities in a) Hartlepool marina (stress 0.29) and b) Sunderland marina (stress 0.11), under different disturbance regimes, based on Bray Curtis similarity coefficient, non standardised data and square root transformed abundances, where: ⊕ - control (group highlighted by dashed circle), + - constant variability, ▲- low variability sequence 1, ■ - low variability sequence 2, ● - low variability sequence 3, △- high variability sequence 1, □- high variability sequence 2, ○ - high variability sequence 3.

In Hartlepool marina SIMPER analysis attributed differences between the undisturbed and disturbed communities to contributions of the dominant species *A. aspersa* in the undisturbed communities and *E. siliculosus* in the disturbed communities. Where *E. siliculosus* was the least dominant species in undisturbed communities, in the presence of a disturbance its relative contribution exploded from 5 % to 34 % replacing *A. aspersa*, which decreased from 38 % to an average contribution of 15 % (Fig. 3.5). All the other species comprising the undisturbed and disturbed communities remained unchanged and with similar abundances despite the disturbance treatment applied. In the presence of disturbances it is also obvious that the total percentage cover of species is reduced by approximately 20 % (Fig. 3.3a).

Table 3.1 – ANOSIM comparing communities undergoing different disturbance regimes in Hartlepool marina, data was non standardised, square root transformed and based on the Bray Curtis similarity, where: A represents constant variability, B represents low variability and C represents high variability of disturbance regime. The numbers 1-3 represent the intrinsic sequence of disturbance events within the disturbance regimes.

	Hartlepool Marina		Sunderland Marina	
Groups	R Statistic	Significance Level (%)	R Statistic	Significance Level (%)
A - B1	0.041	22.4	-0.094	88.1
A - B2	-0.043	69.9	-0.07	75.3
A - B3	-0.031	60.8	-0.053	65.6
A - C1	-0.02	56.9	-0.031	54.1
A - C2	-0.033	64.3	0.173	5.9
A - C3	-0.1	96.7	-0.027	54.2
A - Control	0.331	0.2	0.369	0.4
B1 - B2	-0.041	67	-0.074	74.5
B1 - B3	0.017	35.4	-0.121	92.4
B1 - C1	0.016	35.7	-0.056	61.5
B1 - C2	-0.033	61.8	0.053	23.8
B1 - C3	0.032	27.6	-0.12	96.3
B1 - Control	0.264	1.8	0.261	3.1
B2 - B3	0.009	38.7	-0.132	98.9
B2 - C1	-0.024	61.2	-0.109	91.1
B2 - C2	-0.03	63.9	0.031	32.2
B2 - C3	-0.034	66.4	-0.087	85
B2 - Control	0.256	1.9	0.242	3.1
B3 - C1	0.029	35.9	-0.151	99.4
B3 - C2	0.006	44.8	-0.049	59.8
B3 - C3	-0.074	80.2	-0.128	97.7
B3 - Control	0.457	0.4	0.323	1.5
C1 - C2	-0.096	91.7	-0.069	70.2
C1 - C3	-0.048	68.1	-0.114	90.2
C1 - Control	0.39	0.5	0.276	1.7
C2 - C3	-0.022	57.5	-0.067	70.7
C2 - Control	0.388	0.4	0.312	1.6
C3 - Control	0.307	1.5	0.294	2.2

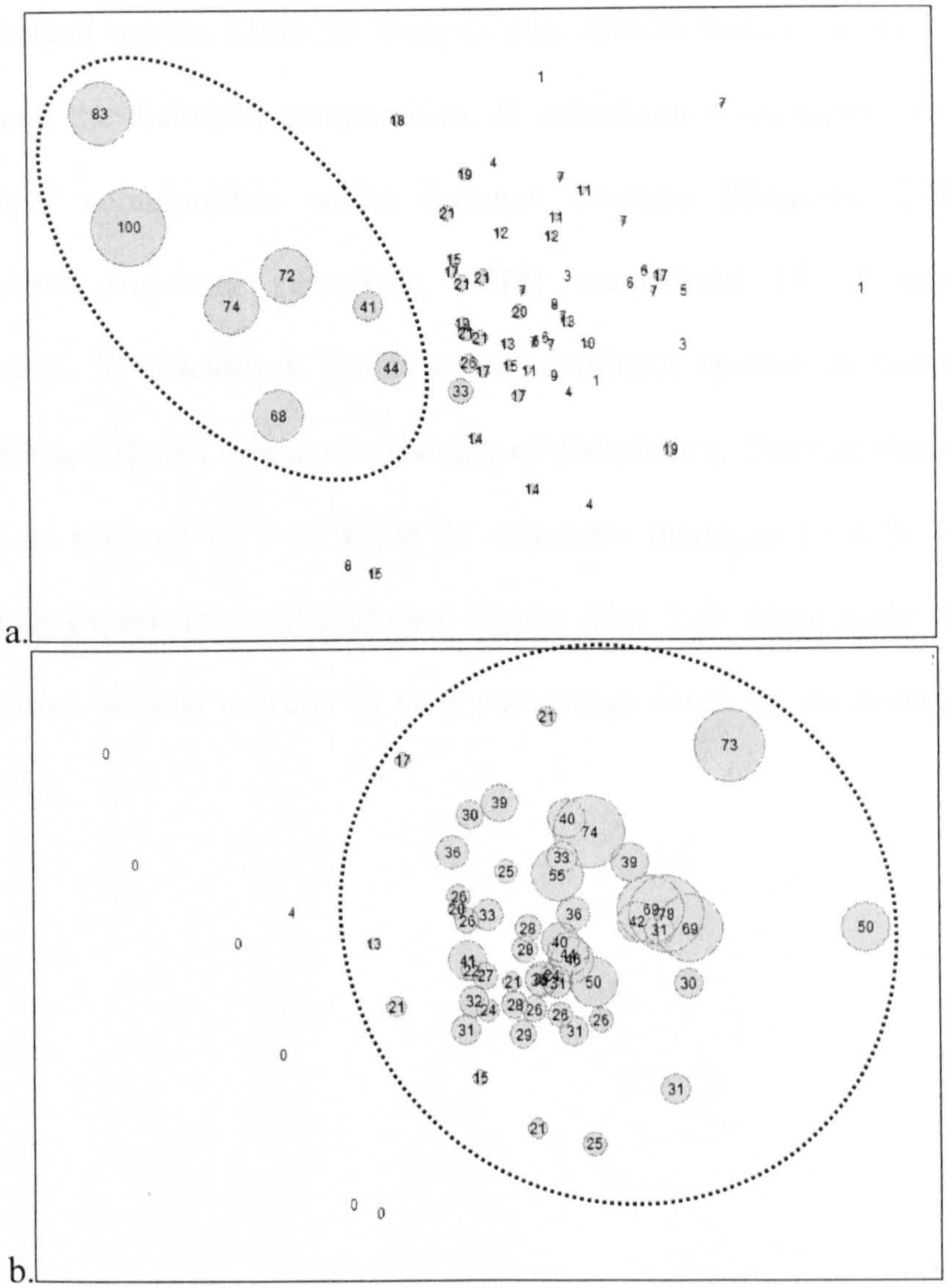


Figure 3.5 – Bubble plots showing contributions of a) A. aspersa and b) E. siliculosus in Hartlepool marina. Values in the bubble plots represent the absolute abundance of the species, while bubble diameter is scaled to the maximum abundance for the species. Dashed circle represents the control group in plot a, and the disturbed group in plot b, there is no distinction between levels of variability as groups were the same. Stress value for both plots was 0.2.

In Sunderland marina SIMPER analysis also ascribe differences between the control and the disturbed communities. *E. siliculosus* contributed 78% in the undisturbed communities, whilst *Balanus crenatus* (Brugiere, 1789) and *Pomatoceros triquieter* (Linnaeus, 1718) contributed 17 % and 5 % respectively. *E. siliculosus* remained the dominant species in communities experiencing different levels of variability of disturbance. The contribution of *B. crenatus* is reduced to 6 % while *P. triquieter* increases to 9 % after the community experienced a disturbance regime (Fig. 3.6). Once again disturbed communities became reduced in total percentage cover by on average 25 % (Fig. 3.3 b).

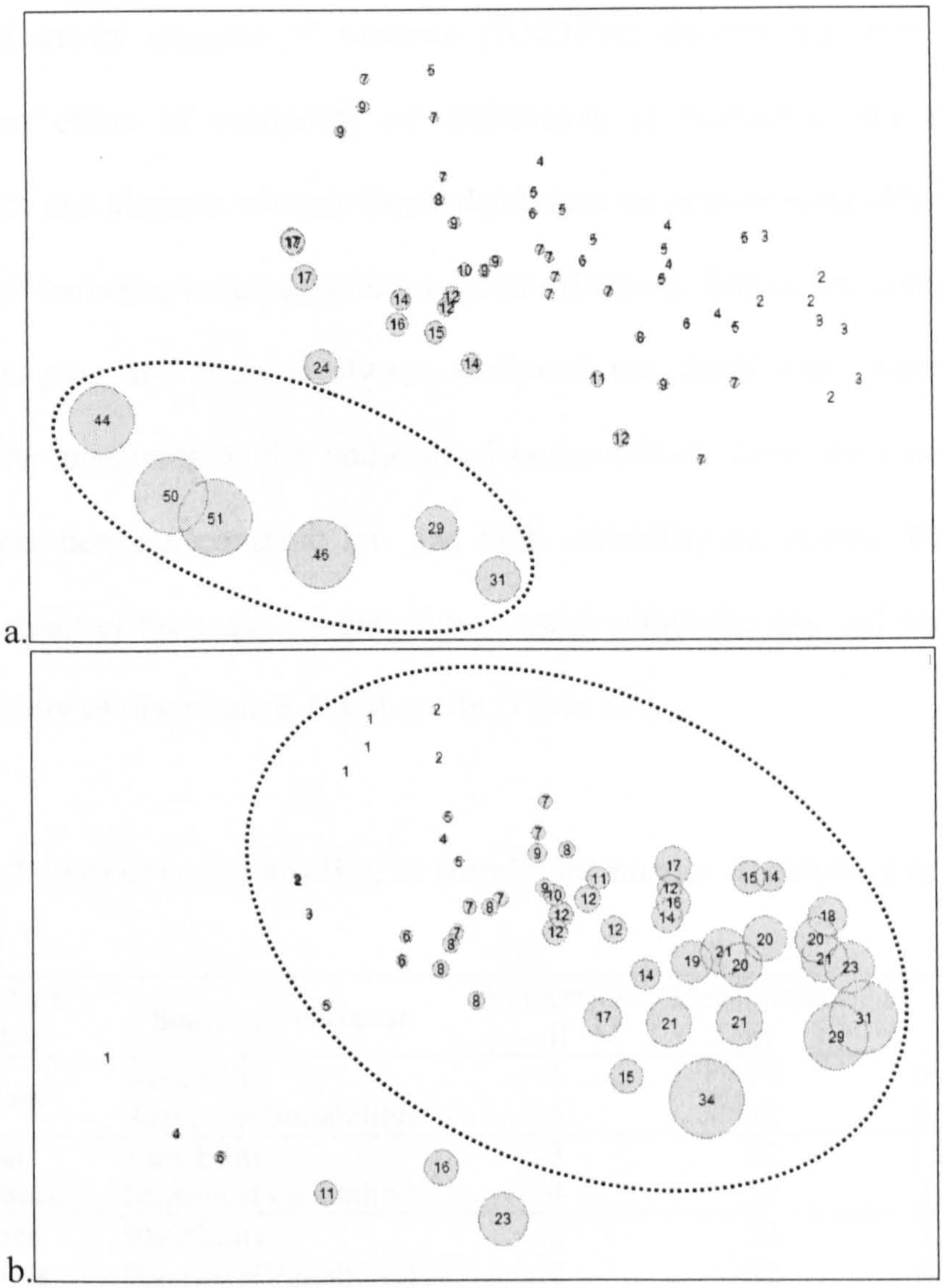


Figure 3.6 – Bubble plots showing contributions of a) B. crenatus and b) P. triquieter in Sunderland marina. Values in the bubble plots represent the absolute abundance of the species, while bubble diameter is scaled to the maximum abundance for the species. Dashed circle represents the control group in plot a, and the disturbed group in plot b, there is no distinction between levels of variability as groups were the same. Stress value for both plots was 0.11.

A mixed model analysis of variance (ANOVA) showed that there was a significant effect of variability of disturbance in Hartlepool on the total abundance and biomass while in Sunderland there were significant effects on all dependant variables tested apart from species richness. Bonferroni comparisons of means *post hoc* analysis always attributed the significant differences in variability treatments to the undisturbed communities, there were never any differences between constant, low and high variability treatments. There was also no effect of the sequence over time, nested within the low and high levels of variability of disturbance, at either site (Table 3.2).

Table 3.2 – Mixed model ANOVA; a) Hartlepool marina, b) Sunderland marina.

a.

Dependant variable	Source of Variation	Numerator df	Denominator df	F	p
Biomass	Variability	3	52	16.699	<0.001
	Sequence(Variability)	4	52	0.372	0.828
Total Abundance	Variability	3	52	11.193	<0.001
	Sequence(Variability)	4	52	2.068	0.098
Species Richness	Variability	3	52	1.117	0.350
	Sequence(Variability)	4	52	0.717	0.584
Evenness	Variability	3	52	1.693	0.180
	Sequence(Variability)	4	52	0.260	0.902
H'	Variability	3	52	2.645	0.059
	Sequence(Variability)	4	52	0.213	0.930

b.

Dependant variable	Source of Variation	Numerator df	Denominator df	F	p
Biomass	Variability	3	52	30.275	<0.001
	Sequence(Variability)	4	52	0.163	0.956
Total Abundance	Variability	3	52	26.233	<0.001
	Sequence(Variability)	4	52	0.688	0.604
Species Richness	Variability	-	-	-	-
	Sequence(Variability)	-	-	-	-
Evenness	Variability	3	52	2.847	0.046
	Sequence(Variability)	4	52	0.788	0.539
H'	Variability	3	52	2.848	0.046
	Sequence(Variability)	4	52	0.788	0.538

NB/ There is no calculation for species richness in Sunderland marina as the number of species was always 3.

In both Hartlepool and Sunderland marina the biomass (dry weight, g) and the total abundance (% cover) were reduced in disturbed communities, since the nature of the disturbance resulted in a loss in biomass (Fig. 3.7; $P < 0.001$, Table 4.2).

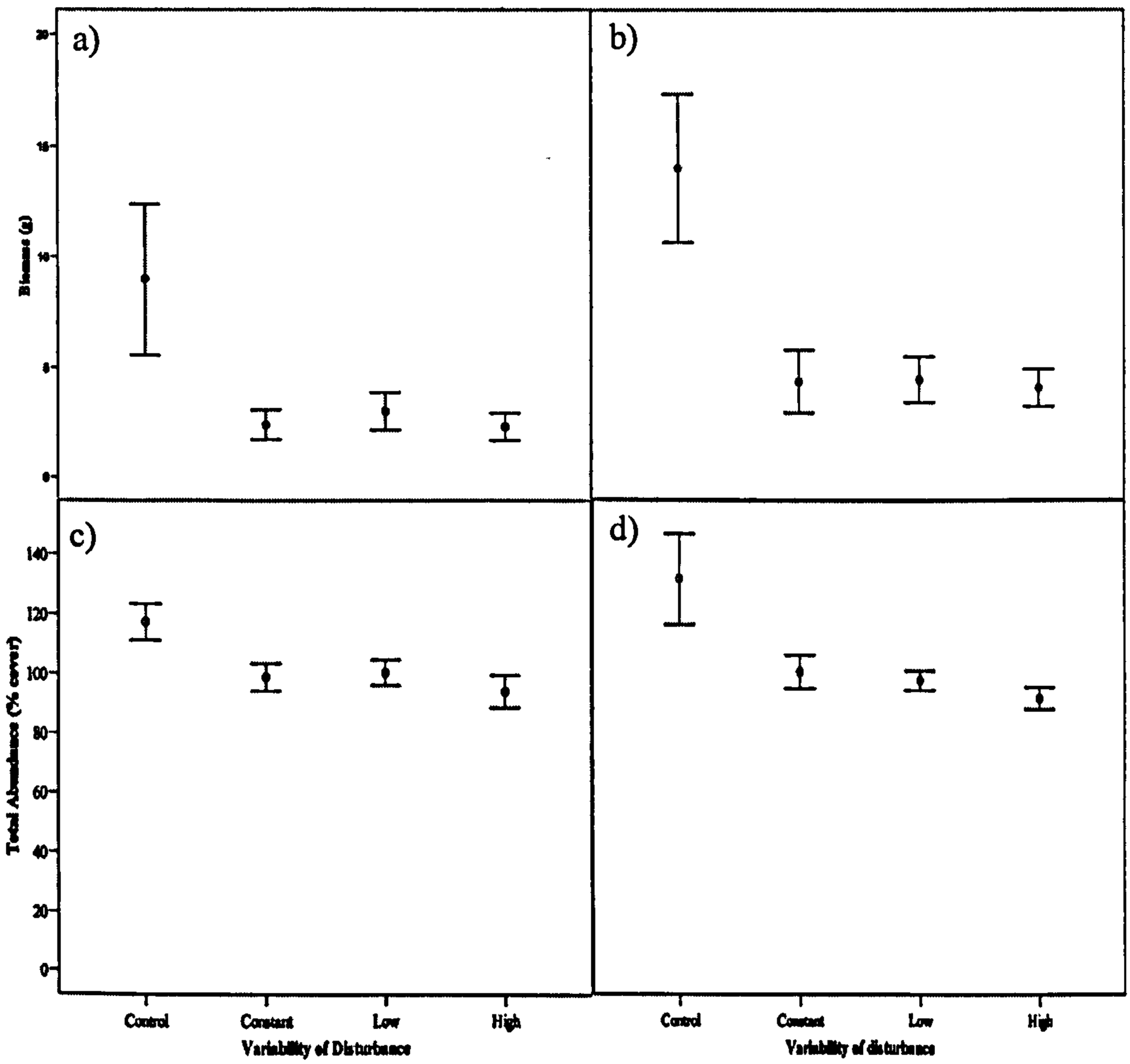


Figure 3.7 Mean ± 1 SE biomass (dry weight (g)) in a) Hartlepool marina and b) Sunderland marina, and Mean ± 1 total abundance for c) Hartlepool marina and d) Sunderland marina, under different variability of disturbance, whisker bars represent the standard error.

In Hartlepool marina, although there was no significant effect of variability of disturbance on the evenness of communities it can be seen from the graph that the evenness of benthic communities is positively affected (Fig. 3.8a), with differences occurring between the undisturbed and disturbed. The increase in evenness is due to the removal, by disturbance events, of the dominant competitor for space *A. aspersa*, as this species is removed the rarer species, e.g. *E. siliculosus*, already present in the community are able to quickly exploit the freed space, and increase in abundance before the ascidians can regain dominance.

In Sunderland marina the variability of disturbance negatively affected the evenness of benthic communities (Fig. 3.8b). Differences in the variability of disturbances were between undisturbed and disturbed communities with no differences between the variability treatments, significantly confirmed in the *Post hoc* test ($P > 0.05$). This is due to disturbance events affecting the subordinate species *B. crenatus* as appose to the dominant competitor for space *E. siliculosus*, therefore increasing the monopoly of *E. siliculosus* in the community by invading the free space created by a disturbance, and reducing the evenness. Species was not significantly affected by disturbances in either marina (Fig. 3.8 c & d).

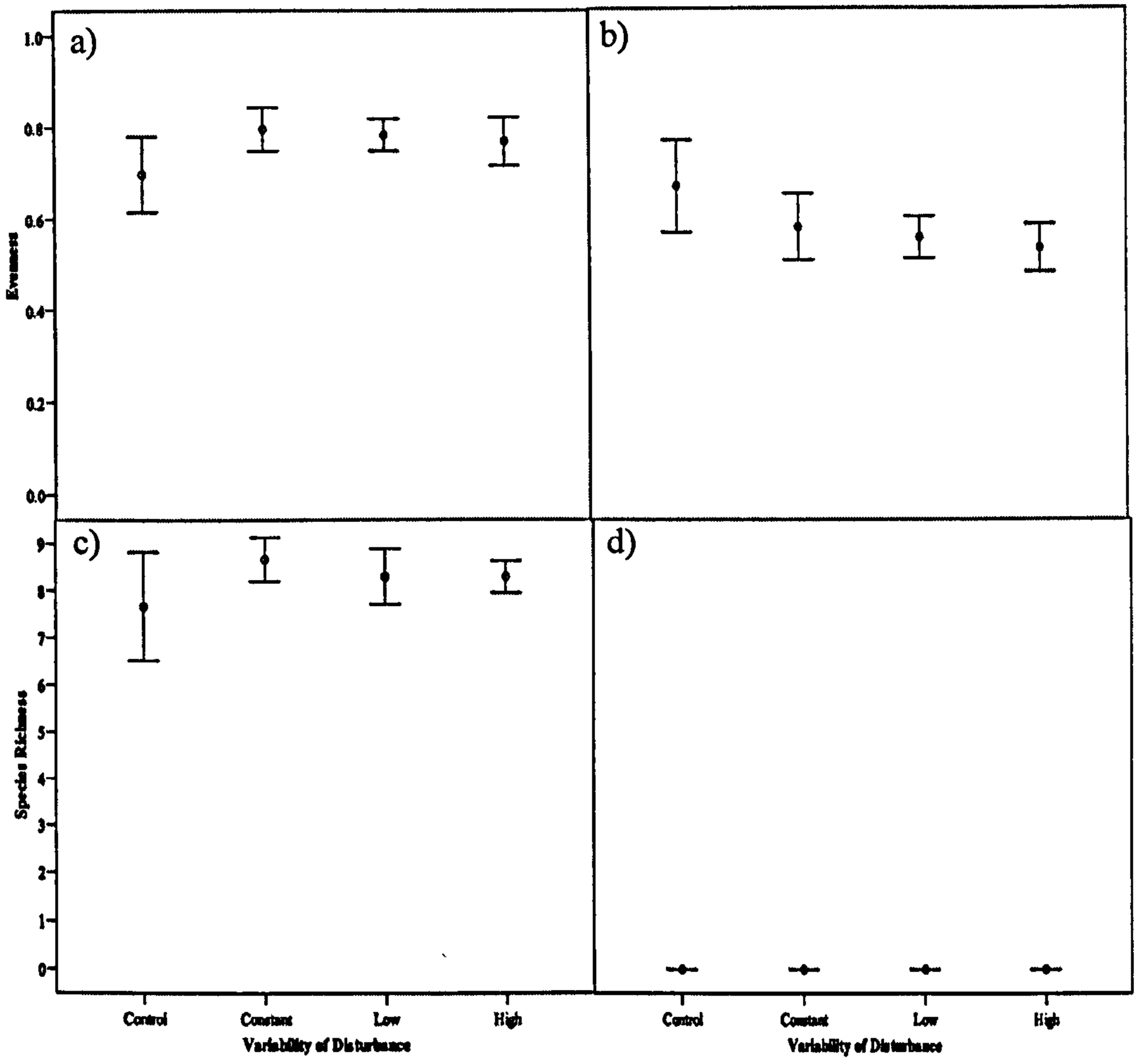


Figure 3.8 –Mean ± 1 SE evenness in a) Hartlepool marina and b) Sunderland marina, and mean ± 1 SE species richness in c) Hartlepool marina and d) Sunderland marina, under different variability of disturbance, whisker bars represent the standard error.

3.4 – Discussion

Benedetti-Cecchi (2003) has been previously suggested that changing the variance around the mean effect size of the predictor variable (i.e. the disturbance regime) can have important consequences for the response of a community assemblage (Benedetti-Cecchi 2003, Bertocci *et al.* 2005) however this has rarely been experimentally tested (cf. Butler 1989, Navarrete 1996, Benedetti-Cecchi 2000). The aim of this study was to investigate whether the temporal variability in a disturbance regime has an effect on the species diversity and composition of marine fouling assemblages. The results presented in this paper show no support for this theory at either of the sites investigated.

It has also been highlighted (McCabe & Gotelli 2000, Bertocci et al. 2005) that within regimes of equal disturbance variability, disturbances may occur in different sized clusters within any one regime. This may have severe implications on the ability of populations to re-colonise disturbed areas, depending on whether the specific timing of clusters coincide with reproduction or recruitment into a community (McCabe & Gotelli 2000, Bertocci et al. 2005). This aspect was investigated by manipulating the specific timing of disturbance events within the two levels of temporal variability and it was found once again that this had no effect on assemblages at either site.

At both study sites, the disturbances applied reduced the biomass and the total abundance of the fouling assemblage. This was expected since the nature of the disturbance was to create a loss in biomass and it was shown very clearly that

there was an effect of the treatment. This effect remained evident because the disturbances were too frequent to allow the complete re-establishment of the fouling community, preventing a subsequent gain in biomass.

Elton (1958) suggested that a decrease in the diversity of a system restricts its functioning and lowers its ecological stability; stability being defined as the resistance of a community despite the presence of a disturbance (Grimm and Wissel, 1997) . To this day, his notion has inspired a great number of studies which both supported (McNaughton 1977, King & Pimm 1983, Tilman et al. 1996) and challenged (DeAngelis 1975, Pimm 1984) the diversity-stability hypothesis. We conclude that the benthic assemblages in Hartlepool, due to the presence of 14 species with different ecological traits, were more stable towards disturbance than the assemblages in Sunderland, since community diversity at Hartlepool marina was maintained in response to disturbances. Former studies revealed that higher plant diversity led to a higher stability of grassland ecosystems towards disturbance (McNaughton 1977, King & Pimm 1983), while, more generally, it has been argued that community stability increases with increasing diversity (Pimm 1984, Odenbaugh 2001). Here the dominant competitor, *Ascidiella aspersa*, was efficiently removed by the disturbance events and could not re-colonize the freed space, while competitively inferior species, e.g. *Ectocarpus siliculosus* and *Botrylloides leachi,* which were already present in the communities, exploited this resource quickly by lateral in-growth. The incapability of the ascidian for vegetative growth and its slow growth rates prevented it from regaining its competitive dominance.

The species-poor assemblages of Sunderland marina appeared to be less stable, since here diversity was decreased by disturbance. This decrease was due to the negative effects of disturbance on the competitively inferior species *Balanus crenatus* and *Pomotoceros triqueter* while the brown algae *E. siliculosus* was favoured. It monopolized the area after a disturbance event because it quickly invaded the free space which was created, which in turn reduced the evenness of the assemblage. The lack of functional diversity, i.e. more organisms capable of lateral growth, in this system made it less stable compared to the fouling assemblages in Hartlepool marina. This observation shows support for the diversity-stability hypothesis (Elton 1958).

Although this experiment was carried out on small local scales it was globally replicated at 16 other sites in 8 countries distributed evenly across the Northern and Southern Hemispheres. Each of these experiments was identical, investigating marine benthic subtidal communities at the same depth. In these experiments it was found that there were always effects of disturbances on the communities but almost unanimously that there were no effects of the variability of the disturbance regime or its sequence (personal communication). Therefore although each individual experiment was on a small local scale, the global replication, which reaches similar conclusions at each site, indicating that there is very strong evidence for the response of this type of ecosystem to variable disturbance regimes.

With a dynamically changing environment and shifting global climate it is predicted that there will be large impacts on ecosystems, owing to the changes

caused by increased sea surface temperatures, rising sea levels and changed patterns of precipitation (Michener *et al.* 1997). One of the most important of these predictions is that the intensity, frequency, distribution and seasonal duration of large disturbances, such as hurricanes, tropical storms and periods of extreme heat, will become more variable and severe, with a clustering of events in short periods separated by large intervals (Smith & Buddermeier 1992, Michener et al. 1997). If this is the case then predicting the effects of a variable disturbance regime could be a very important tool to protect and conserve biodiversity.

In conclusion, it seems that although the inherent variation and sequence of disturbance events do not affect benthic assemblages of an early successional stage in the temperate subtidal systems investigated herein, disturbance events in general do, and they are an important force in structuring community assemblages. However, although there was no effect on the systems investigated this may not, nor should be taken as, the case for all types of assemblages. It is possible that this could be due to the confounding effects of recovery from recent disturbances to the point of sampling, for example, by having regular sampling throughout the study and taking the average response of assemblages we could gain a more thorough interpretation of the experimental treatments, better enabling the effects of variance and sequence to be separated from the recent history of disturbances. It seems that in marine hard bottom assemblages, diversity is increased under the influence of disturbances adding support to the non-equilibrium concept of biodiversity. However, although variation within communities is the cornerstone of this paradigm (Landres *et al.* 1999) it seems,

in this case, that the variability in the driving force, i.e. the disturbance regime, is unimportant. In terms of diversity the most crucial aspect was the actual disturbance itself.

Chapter Four: The role of refuges in maintaining species diversity with abiotic disturbances

4.1 – Introduction

Habitat complexity is ecologically important and has been implicated as a driving force within ecological communities nearly as often as competition (Petren & Case 1998, McAbendroth et al. 2005). Species diversity has been positively correlated with habitat complexity in many aquatic and terrestrial systems (Petren & Case 1998, Johnson et al. 2003), an association known as the habitat-diversity hypothesis (Debski et al. 2002). In the past this was one of the reasons that many provided for the co-existence of species under the equilibrium concept of species diversity (Hardin 1960, Connell 1978), but with emphasis shifting to the viewpoint that ecological communities are continually changing (Collins & Glenn 1997), the importance of habitat complexity seems to have become lost.

At local scales habitats with a greater structural complexity are thought to increase diversity by providing a greater number of structural niches for exploitation by different species with different life history characteristics. This results in changes in resource partitioning and niche breadth (McAbendroth et al. 2005), modification of biotic interactions and altered community structure (Raffaelli et al. 2000, Schmid 2000). Therefore, facilitating the settlement and persistence of many species in an environment where they would have been otherwise out-competed, increasing co-existence (Kostylev et al. 2005). The combination of these structural niches leads to complex or heterogeneous environments but the terms are often confused leading to difficulties when

investigating this driving force (Beck 2000). In order to avoid confusion at this point a definition of the terms used herein can be found in Table 4.1.

Table 4.1 – Definition of terms

Term	Definition
Surface complexity	A measure of the structure of a surface taking into account the absolute abundance of the distinct physical elements making up the surface
Surface heterogeneity	The variation in the relative abundance of different structural components within a surface
Habitat	The living place of an organism or community characterised by its physical and biotic properties
Niche	The functional position of an organism within its habitat, comprising the area in which the organism lives, the time it occurs and the resources both biotic and abiotic it contains
Structural Niche	The area in which an organism can live within its habitat, comprised solely of the physical surface on which it could live
Refuge	A site defined in space and time within which particular organisms are sheltered from biotic and abiotic disturbances

Marine habitats are characteristically dynamic where many species survive despite several causes of biotic and abiotic mortality (Frost et al. 2005). Rocky shore habitats whether intertidal or subtidal are extremely heterogeneous, at both small and large scales, and they provide a number of niches available for colonization. The heterogeneous nature of these niches provides an array of structural niches, which act as refuges against predation, competition and

disturbance (Connell 1961, Walters & Wethey 1996, Beck 1998, Bergey 2005, Frost et al. 2005). An increase in structural niches often provides the only means of survival to organisms who are otherwise unable to reduce mortality in response to these factors (Connell 1961, Menge & Lubchenco 1981, Gillinsky 1984, Bergeron & Bourget 1986, Walters & Wethey 1996). This ultimately results in a habitat with extremely high diversity (Johnson et al. 1998, Denny 2006).

Structural niches can be further defined as refuges by the specific topographic features that are found within them, such as crevices. Refuges with pits and crevices are thought to offer protection against predation and disturbances (Keough & Downes 1982, Barry & Dayton 1991), whilst the peaks associated with them offer an area of settlement for species that cannot compete for space. The success of each of these species will depend on their life history characteristics, as well as their tolerance of the other external factors associated with each of the refuges (Connell & Keough 1985, Walters & Wethey 1996). However the effects of both complex and heterogeneous habitats will always be scale dependent (Beck 2000).

The concept of refuges implies protection against an agent of mortality and it is therefore essential to define the type of mortality to which a refuge is being provided (Berryman & Hawkins 2006). Disturbances (as defined in Section 1.6.1) are major forces in the structuring and development of communities in all types of habitats (Connell 1978, Sousa 1984). Abiotic disturbances in marine habitats are particularly important in the development of sessile benthic

communities because they effectively open up free space, a common limiting resource, and allow the establishment of species that could have potentially been out-competed, therefore increasing community diversity (see Chapter 2 & 3). Common types of abiotic disturbances in rocky shore habitats include physical disturbances such as crushing and impaction (Dayton 1971), increased hydrodynamic shear from increased wave action during storms (Denny 1994), and desiccation stress in the intertidal zone (Anthony & Kerswell 2007). Physical disturbances resulting in direct crushing and a loss in biomass from a portion of the community have already been discussed in detail in chapters 2 and 3.

Water flow is another important force in structuring the marine environment; it influences the distribution of organisms, the transportation of nutrients and energy, as well as disturbance regimes (Hart & Finelli 1999). Despite its importance water flow can also constitute an important disturbance onto benthic organisms imposing hydrodynamic shear which results in increased drag and lift as the water velocity increases (Denny 2006). Most benthic organisms are adapted to the local physical conditions in which they live; they are able to move with the flow of water negating the effects of hydrodynamic shear. However with extreme increases in the shear imposed on these organisms resulting from extreme storms the ability to counteract water flow will only be effective up until a point where dislodgement becomes inevitable. The effects of water flow on benthic organisms has been extensively investigated (Denny 1994, Walters & Wethey 1996, Koehl 1999), and the extent of the forces

imposed by water motion can, with caution, be accurately predicted (Denny 1988, Kawamata 1998, Gaylord 2000).

Organisms living in the intertidal zone have to survive in one of the most challenging physical environments in marine habitats; they experience extreme temperatures, potentially high solar radiation and water loss on a daily basis (Helmuth 1998, Anthony & Kerswell 2007). Desiccation stress is therefore a vital factor in influencing the vertical distribution of organisms on rocky shores, often resulting in clear patterns of zonation in direct response of an organism to tolerate exposure from the water (Connell 1961).

Species will respond to each of these disturbances in very different ways. Physical disturbances are by their nature random, occurring by chance with different frequencies and intensities, due to varying spatial and temporal factors, making them and the responses associated with them very hard to predict. Hydrodynamic shear is more uniform, changing with changing water velocities, which are easier to determine than the associated physical disturbances. Though easier to predict they are also temporally variable becoming more random with changing seasons. Desiccation stress, however, is very uniform and therefore very predictable, occurring at a set time, for a known period of time every day. The response of organisms to desiccation stress is also therefore much more predictable than for the other types of abiotic disturbances.

With the ever increasing threat of global change all of these disturbances are thought to become more frequent and intense (see section 1.2.5); therefore

changing the predicted response of communities that have previously appeared well adapted and relatively stable. But it is not just the climate that is changing and threatening the survival of species in marine habitats. Increased modification of coastal habitats has transformed natural shores into urbanised areas of artificial structures which host different species assemblages than those on the natural shores, whilst providing available areas for the invasion of exotic species, adding to the homogenization of the World's biota. It is increasingly essential to understand the effects of habitat complexity on the dynamics of species diversity and disturbances in order to promote the management of marine systems and maintain the diversity that is left.

The complex nature of rocky shores and the refuges provided by this complexity are thought to ameliorate some of the stresses associated with the abiotic disturbances in this environment (Gosselin & Chia 1995, Bergey 2005). Bergeron and Bourget (1986) highlighted the value of crevice refuges to the survival of barnacles against ice scour and despite the majority of work agreeing with the vast array of theoretical work in this area there has been little empirical work carried out (Witman 1985, Petren & Case 1998), and the value of topographic refuges in response to abiotic disturbances is largely unknown (cf. Menge 1978, Woodin 1978).

This chapter aims to investigate whether an increase in the structural complexity of a surface increased species diversity with three types of abiotic disturbances: exposure, physical disturbances and hydrodynamic shear in rocky shore habitats. The experiments also aimed to discover whether the composition of the

community structure altered under increased levels of surface complexity in response to the different disturbances. Finally the experiments sought to quantify the structural niches within each level of surface complexity and determine whether there was any relationship between the type of structural niche available for settlement and the species that settled there, to discover if a particular species preferred to settle in a particular type of niche, therefore gaining a refuge in this area from the disturbances that were imposed upon them.

4.2 – Materials and Methods

4.2.1 - Experimental Approach

Three experiments were run using different types of abiotic disturbances (desiccation, physical disturbance and hydrodynamic shear) which were imposed on benthic communities that had been allowed to grow on identical replica rocks. Disturbance frequency was fixed and informal comparisons between experiments were made.

4.2.11 – Manufacture and characterisation of replica rocks

Natural rocks were used to create artificial settlement surfaces in order to gain a natural level of complexity that would not be achieved by using man made surfaces (Hills & Thomason 1998). Four rocks were chosen from the North East coast to provide a natural range of surfaces typical of the area, the type of rock chosen was not important as the chemical nature of the rock does not carry through to the casting stage. The rocks chosen were the smoothest possible and the roughest possible with two intermediate levels and were called R1, R2, R3 and R4 respectively (Fig. 4.1).

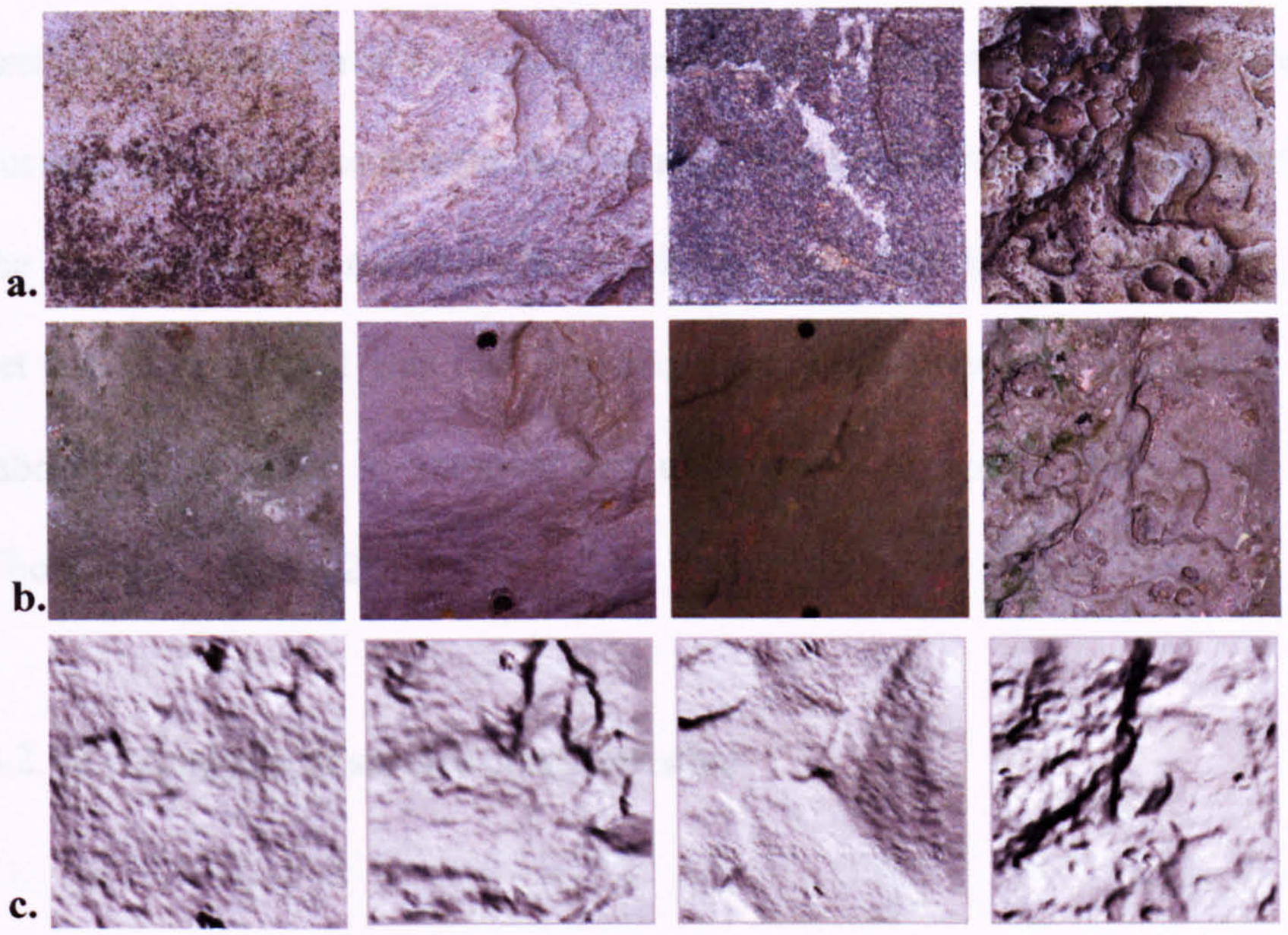


Figure 4.1 – Natural rocks (a.), rock casts (b.) and surface scans composed from the Proscan surface mapping (c.), for each level of surface complexity where casts were 100 x 100 mm in size.

Moulds of the natural rocks were then taken using Extrude Wash polyvinylsiloxane impression material (Kerr Corporation Ltd), a 10 x 10 cm square was laid out onto the surface of the rock using plasticine and impression material was laid inside the template to create a sub-micron impression of the natural rock (Marrs et al. 1995). Once a detailed impression of the rock was obtained a hole punch was used to provide a hole (0.5 cm in diameter), in the centre of the top and bottom edges of each panel, for attachment to the experimental frame with cable ties.

Filled casting epoxy resin FC 702 PA (Trylon Ltd) was then used to create high precision replicas (grey in colour) of each surface. Filled casting resin was used because it contains carbonate dust which has a high surface energy, mimicking the physical and chemical characteristics of natural rocks. The resin was left to set for 12 hours and was then leached for a week under running water in the laboratory in order to remove any unpolymerised resin (Hills et al. 1998, Thomason et al. 2002).

4.2.12 – Analysis of surface characteristics

Once the replica surfaces had been manufactured the characteristics of each of the surfaces was measured. The heterogeneity was quantified as R_a values using the Proscan 2000 Profilometer which provided a precise profile at a resolution of 5nm (Scantron Industrial Products Ltd: Table 4.2). From the scans the precise xyz data for each of the surfaces was obtained. Two- dimensional profiles of the surfaces were then made and the fractal dimension (D), using ImageJ FracLac 2.5 release 1b5i, was also calculated for each surface. In this way a range of roughness parameters were obtained for each level of surface complexity in order to prevent confounding these the effects of heterogeneity and complexity (Kostylev et al. 2005).

Table 4.2 – Roughness parameters where Ra is the average heterogeneity and D is the average fractal dimension for each level of surface complexity

Surface Complexity	Ra	D
R1	531.5	1.124
R2	1193.1	1.074
R3	1119.4	1.121
R4	2506.2	1.122

4.2.13 – Structural Niche Classification

The initial settlement of individual species in relation to the different structural niches, as refuges, available within each of the different levels of complexity was investigated. A biological index similar to that described by Hills & Thomason (1996) was used to discover the potential settlement sites (PSS) for the species' within the benthic community. The refuge index that was created here was classified on a size scale for the larvae due to a paucity of data for the behaviour of all species apart from barnacles. In order to achieve this it was first necessary to describe the different types of structural niche that comprise the topographic complexity within each of the replica surfaces. The method of estimating percentage cover of species (see section 4.2.4) uses a grid overlaid onto photographs of the communities on each of the panels (Fig. 4.2); this grid was used to pinpoint the location of each of the areas that were to be described as the structural niches. Each structural niche was described by graphing the relevant section of the panel to create a 2 x 2 mm cross section (classified according to the categorical system shown in Table 4.3) to match the largest larvae from the species pool in the experimental area (Table 4.4). The frequency

of occurrence of each structural niche within each treatment can be seen in Table 4.5 whilst the locations of each of these niches on the panels can be seen in Fig. 4.3.

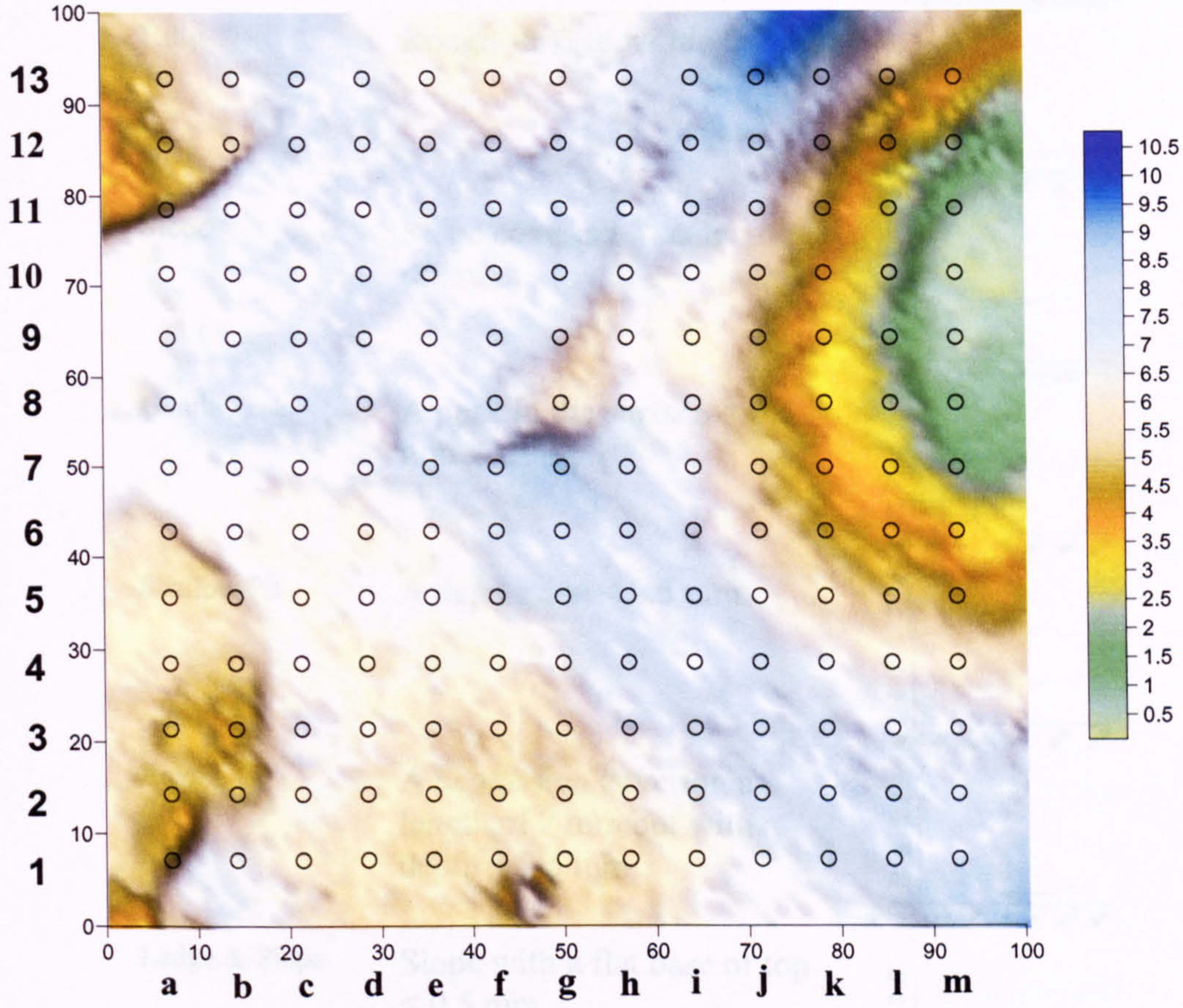
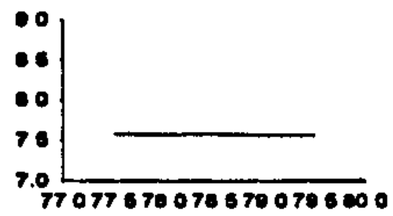
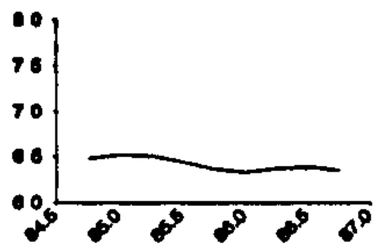
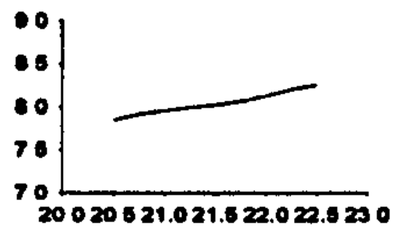
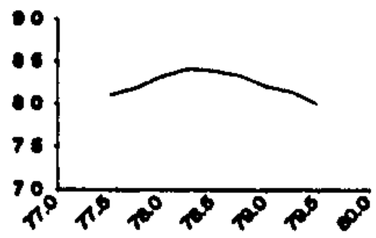
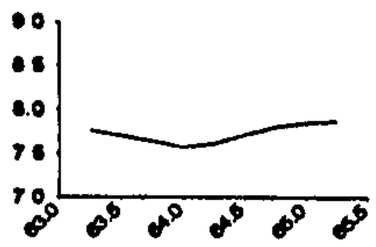
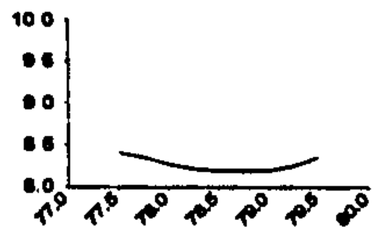
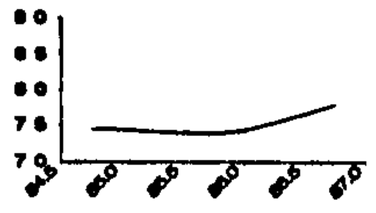
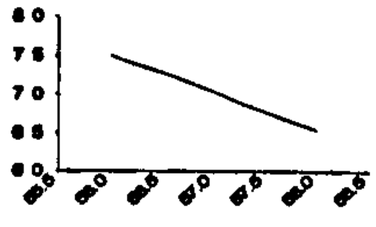
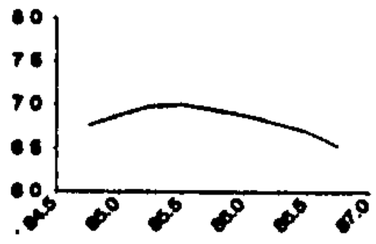
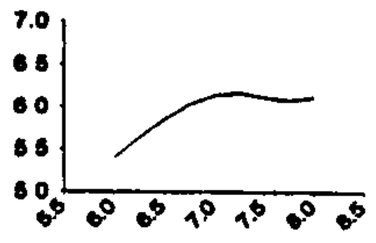
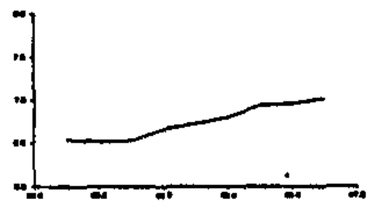
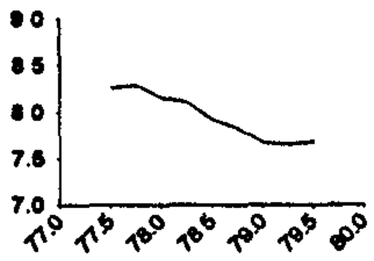
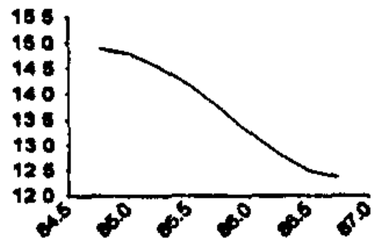
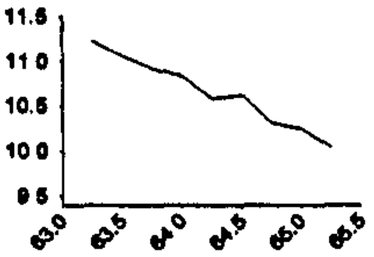
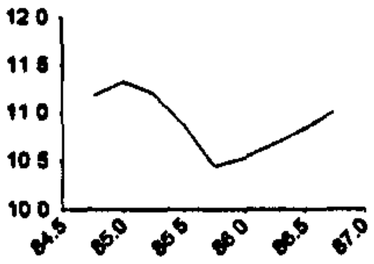
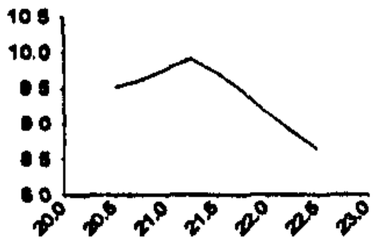
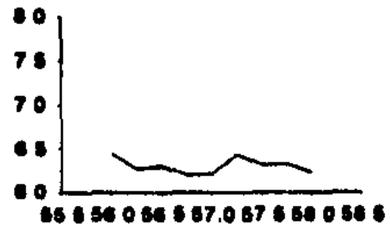
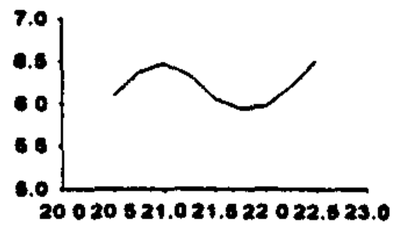
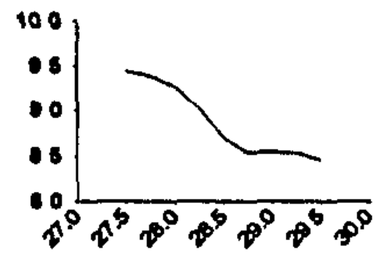
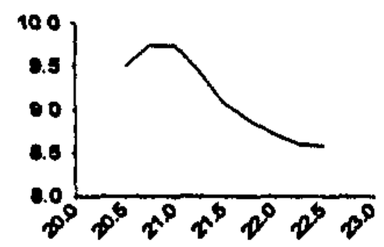


Figure 4.2 – Sampling grid digitally overlaid onto an example scan of a panel, dots represent the location of the area used to identify the niches and consequently the areas where species were counted. Scale bar indicates height (nm) of topographic structures on the panel; green being depressions such as crevices and blue being elevations such as peaks. Axes are in mm and grid reference points are shown.

Table 4.3 – Classification of the structural niche within replica surfaces, an example of the niche available for potential settlement is shown.

Refuge	Description	Example
Flat	Flat surface within 0.2mm	
Hilly	Rough surface within 0.2 mm	
Slope	Slope covering a scale <0.5mm	
Gentle Peak	A peak in the surface < 0.5 mm	
Shallow Pit	A depression < 0.5 mm	
Bowl	A depression covering a length of 2 mm but with a depth < 0.5 mm	
Ledge & Slope	Slope with a flat base or top < 0.5 mm	
Incline	Slope covering a scale > 0.5 mm <1 mm	
Hill	A hill in the surface ≤ 0.5 mm	
Uphill to peak	Upward slope to a peak > 0.5 mm < 1 mm	

Uphill flat base	Upward slope to a flat ledge > 0.5 mm < 1 mm	
Medium ledge & incline	Slope with a flat base or top > 0.5 mm but < 1 mm	
Steep incline	Slope covering a scale > 1mm	
Step up crevice & peak	Depression and hill creating an upward/downward surface > 0.5 mm	
Crevice	Large depression > 0.5 mm	
Peak	Large hill > 0.5 mm	
Medium Hilly	Rough surface ≤ 0.5 mm	
Crevice & Peak	Depression and hill > 0.5 mm	
Steep incline & Ledge	Steep incline with a ledge occurring either at the top or bottom of the incline > 1mm	
Steep Incline & Peak	Steep incline with a peak occurring either at the top or bottom of the incline > 1mm	

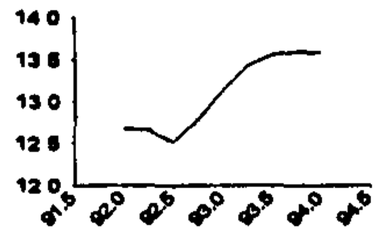
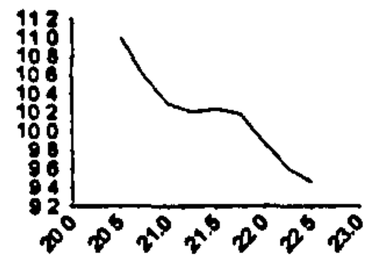
Steep incline & crevice	Steep incline with a crevice occurring either at the top, bottom or within the incline > 1mm	
Double incline & ledge	Flat ledge occurring in two steep inclines > 1 mm	

Table 4.4 – Characteristics of the larvae and spores of the benthic invertebrate and macroalgae community at Low Newton by the Sea (data summarised from Clayton 1992, Young et al. 2002, Marlin 2007)

Phylum	Species	Larvae/Spore Growth Form	Sociability	Body Size Range (µm)
Chlorophycota	*Ulva lactuca*	Zoospore		11 – 12
	Ulva intestinalis	Zoospore		<150
	Enteromorpha linza	Zoospore	gregarious	
	Cladophora rupestris	Zoospore		<60
Rhodophycota	*Palmaria palmata*	Zoospore		
	Ceramium rubrum	Carospore		<50
	Porphyra umbilicalis	Zoospore		
	Plocamium cartilagenium	Zoospore		
Chromophycota	*Saytosiphon lamentaria*	Zoospore		
	Chorda filum	Zoospore	N/A	100
	Fucus serratus	Egg	N/A	64 -250
	Fucus spiralis	Egg	N/A	67 – 70
	Fucus vesiculosus	Egg	N/A	
	Ectocarpus siliculosus	Zoospore	N/A	7 – 10
	Laminaria digitata	Zoospore	N/A	α 5
	Laminaria hyperboria	Zoospore	N/A	α 5
	Laminaria saccharina	Zoospore	N/A	
	Himanthalia elongata	Zoospore	N/A	200
	Alaria esculenta	Zoospore	N/A	α 5
Porphyra	*Halichondria panacea*	Globose	Solitary	α 1000
Bryozoa	*Bugula spp*	Bullate/ saccate	Solitary	180 – 400
	Umbonula littoralis	Globose	Solitary	<800
	Membranipora membranacea	Coronate/ crustose	Solitary	300 – 400
Annelida	*Pomotoceros triqueter*	Globose	Solitary	40 – 500
Crustacea	*Balanus crenatus*	Articulate	Solitary/ gregarious	280 -910
	Semibalanus balanoides	Articulate	Gregarious	α 1000
	Chathamalus montagui	Articulate	Solitary/ gregarious	500
Chordata	*Botryllus sclosseri*	Tadpole	Solitary	500
	Botrylloides leachi			
	Didemnum spp			

Table 4.5 – Frequency of occurrence of each structural niche on each level of surface complexity where: · = 1%, • ≤ 10%, • ≤ 20%, • ≤ 30%, ● ≤ 40%, ● ≤ 50%, ● > 60%.

Refuge Type	Frequency of refuge occurrence:			
	R1	R2	R3	R4
Flat	•	•		
Hilly	●	●	•	
Slope	•	●	•	•
Gentle Peak	•		•	
Shallow Pit	●	·	•	•
Bowl	·	•	•	•
Ledge & Slope	●	●	•	•
Incline		●	•	·
Hill		•		
Uphill to peak		•	•	·
Uphill flat base		•	•	•
Medium ledge & incline		·	•	•
Steep incline		·	•	●
Step up crevice & peak			●	•
Crevice			•	•
Peak			•	•
Medium Hill			●	●
Crevice & Peak			•	•
Steep incline & Ledge				•
Steep Incline & Peak				•
Steep incline & crevice				·
Double incline & ledge				•
Number of refuges	8	12	16	18
Refuge Index	9.81	17.01	7.75	23.83

Once the structural niche on each of the replica surfaces had been classified, a refuge index (RI) was calculated following the formula:

$$\text{Refuge Index} = \frac{\Sigma\,(H \times S \times F)}{\text{No. refuges}}$$

Where H is the maximum height (cm), S is the maximum slope and F is the frequency of occurrence of each refuge within each surface.

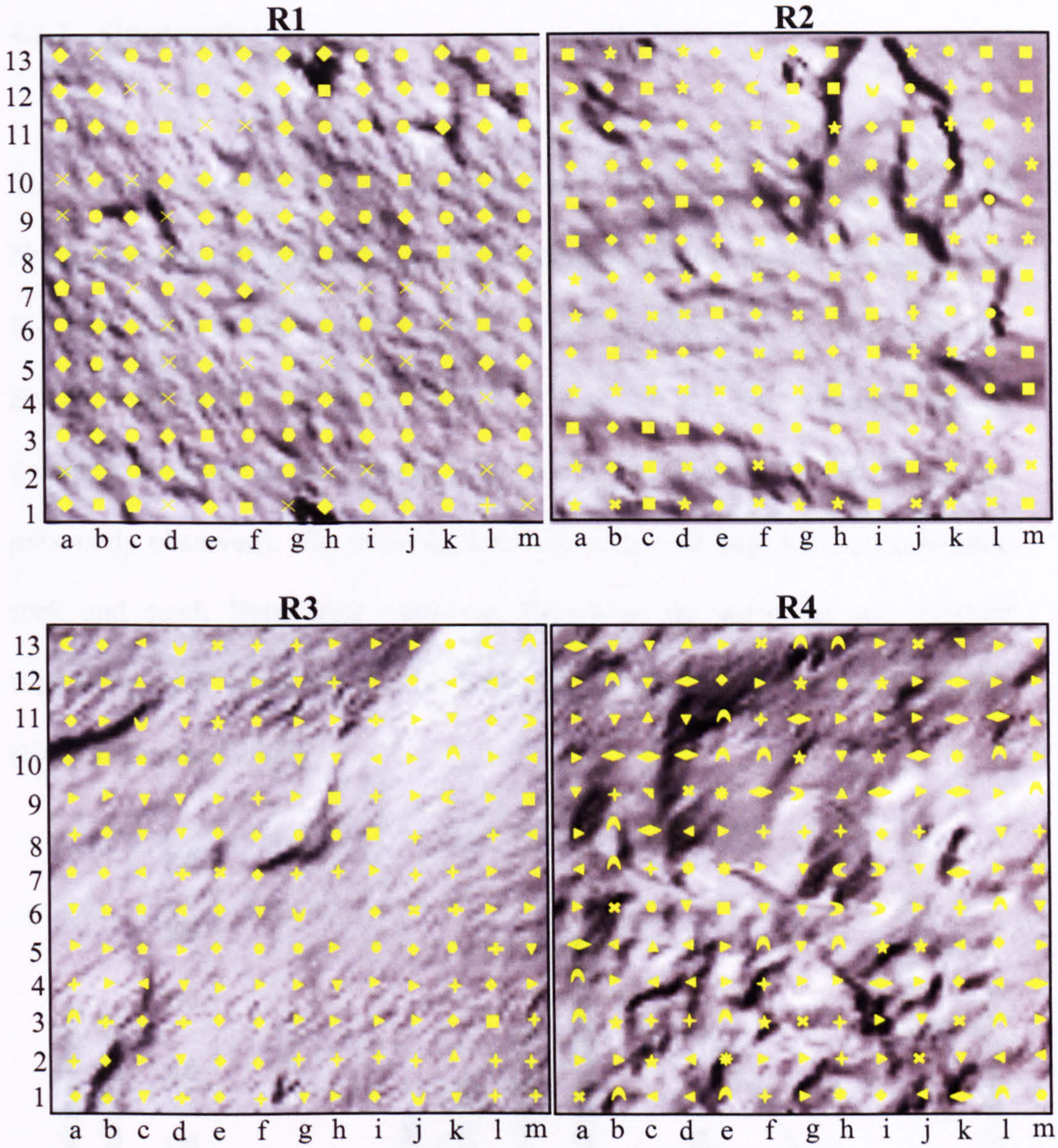


Figure 4.3 – Schematic diagrams showing the locations of the structural niches on the different levels of surface complexity where; 1-13 and a-m correspond to the grid points whilst the symbols within the grid correspond to the type of niche located at this point:

- *Flat*
- *Bowl*
- *Uphill flat base*
- *Peak*
- *Steep incline & crevice*
- *Hilly*
- *Ledge & Slope*
- *Medium ledge & incline*
- *Medium Hill*
- *Double incline & ledge*
- *Slope*
- *Incline*
- *Steep incline*
- *Crevice & Peak*
- *Gentle Peak*
- *Hill*
- *Step up crevice & peak*
- *Steep incline & Ledge*
- *Shallow Pit*
- *Uphill to peak*
- *Crevice*
- *Steep Incline & Peak*

4.2.2 - Site description

The experiments were carried out from March 2006 until October 2006 on the North East coast of England (environmental data for this region is displayed in Fig. 4.4). Experiments were deployed in a sheltered bay at Low Newton by the Sea (55° 30' 41.52'' N, 1° 36' 35.52'' W: Fig. 4.5), an area with high species diversity compared to the majority of the North Sea coast (Table 4.6: 50 species personally observed). The area has a mix of substrata: both hard metamorphic rock and sand. Hard rock reefs are diverse in the intertidal and subtidal supporting rich communities, including those associated with kelp forests (Natural-England 2007).

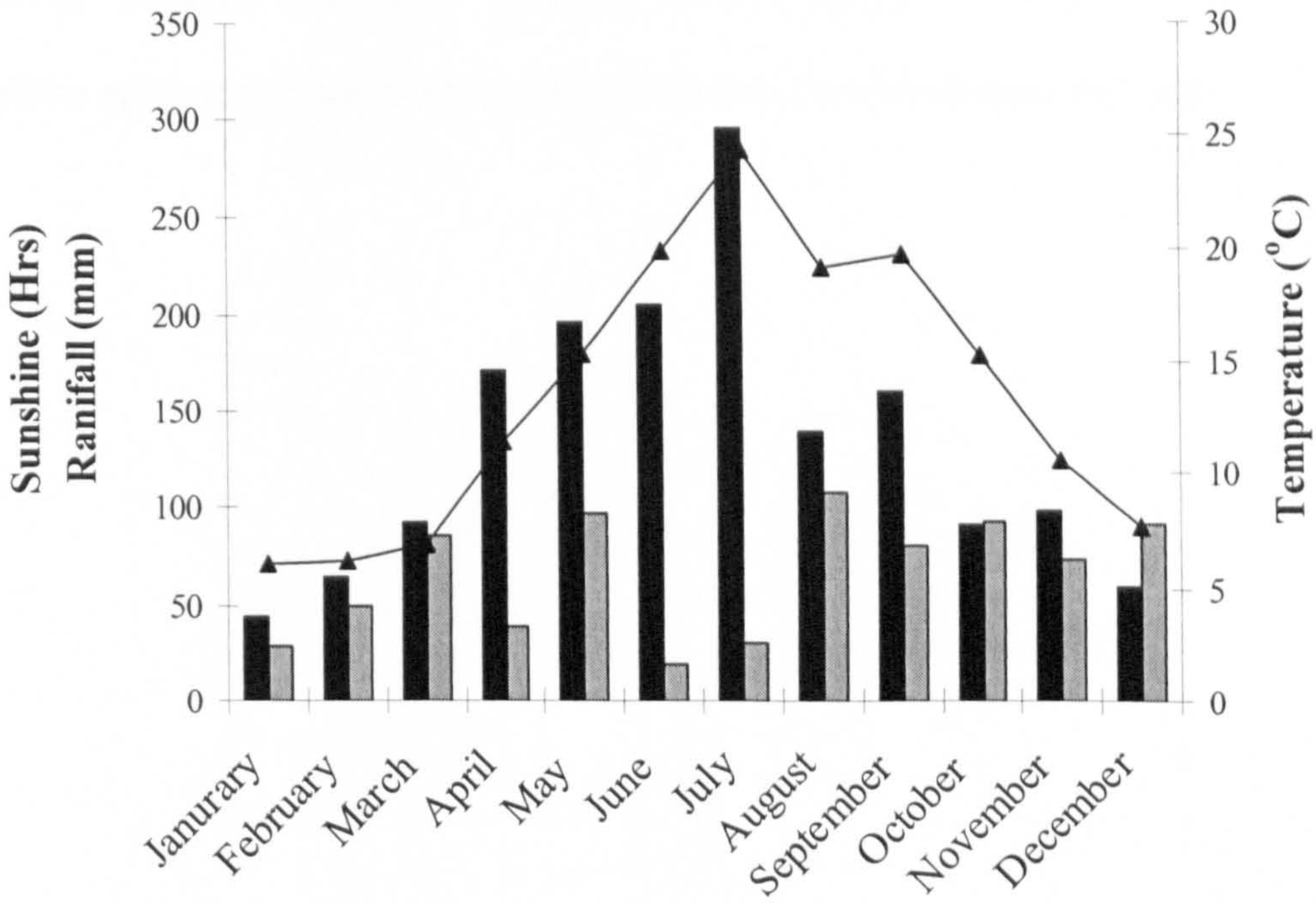


Figure 4.4 – Average sunshine (hours: black columns), rainfall (mm: grey columns) and temperature (°C: black line) for North East England, 2006 (MeteorologicalOffice 2007, Metoffice 2007)

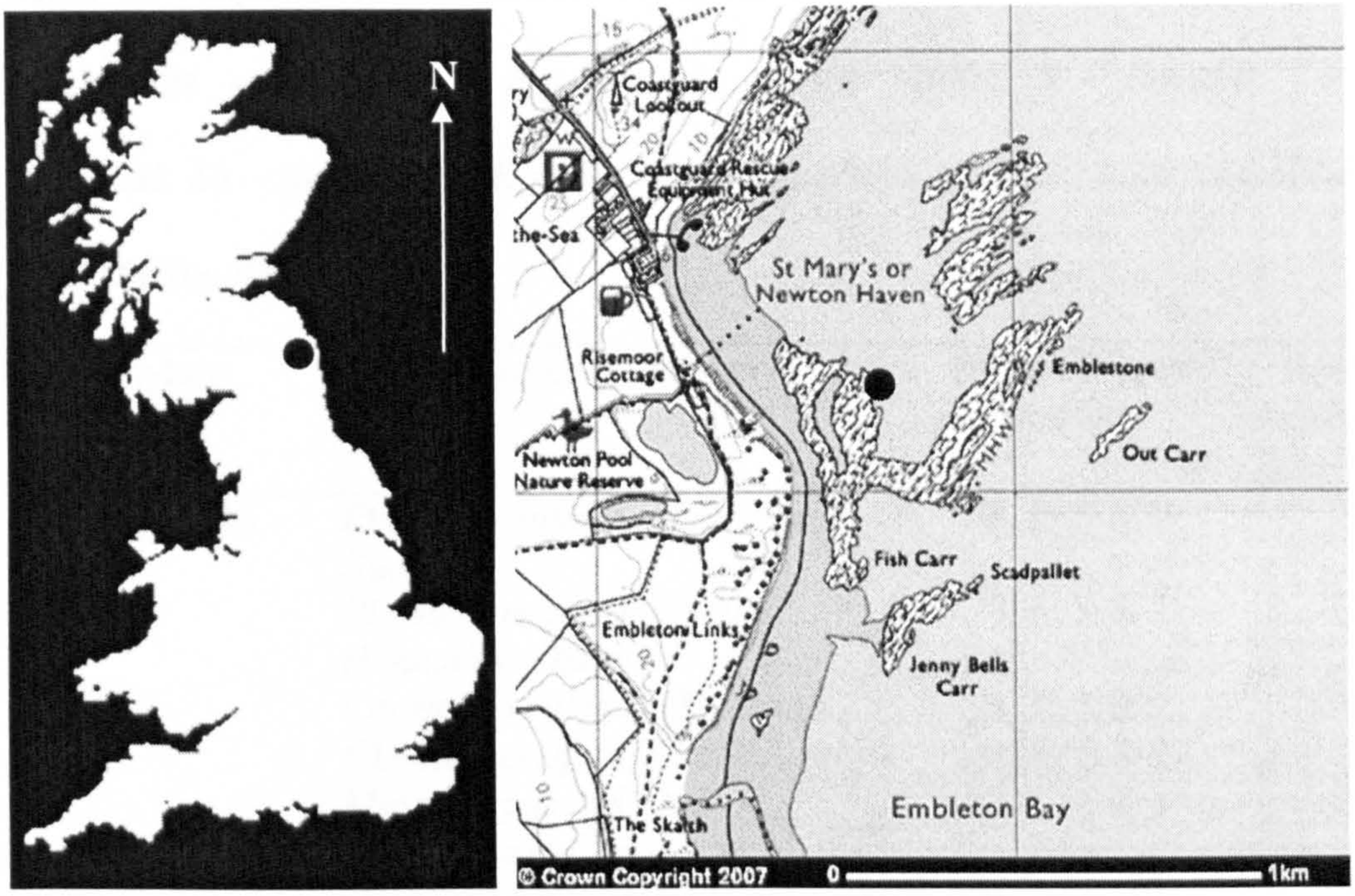


Figure 4.5 – Location of study site Low Newton by the Sea on the North East coast of England, black dots represent the location of the site as well as the location of the experiments within the site (taken from Ordinance Survey).

Table 4.6 – Natural marine community at Low Newton by the Sea, where: B – benthic; M – mobile; E – Epi -benthic, -phytic ,-lithic; S – subtidal; I – intertidal; Sh – sheltered; ME & HE – moderate high exposure (data compiled from Marlin 2007)

Phylum	Species & authority	Environmental position	Present in experimental communities
Rhodophycea	*Palmaria palmata (Linnaeus) Kuntze*	B, E, S & I	Yes
	Plocamium cartilagineum (Linnaeus) Dixon	B, E, S & I	Yes
	Ceramium rubrum (Hudson)	B, E, S & I	Yes
	Chondus crispus (Stackhouse)	B, E, S & I	No
	Mastocarpus stellatus (Stackhouse) Giury	B, E, S & I	No
	Porphyra umbilicalis (Linnaeus) Kutzing	B, E, I, HE	Yes
Chlorophycea	*Ulva lactuca (Linnaeus)*	B, E, S & I, Sh	Yes
	Ulva intestinalis (Linnaeus)	B, E, S & I	Yes
	Enteromorpha linza (Linnaeus)	B, E, S & I	Yes
	Cladophora rupestris (Linnaeus) Kutzing	B, E, S & I	Yes
Chromophycea	*Scytosiphon lomentaria (Lyngbye)*	B, E, S & I	Yes
	Chorda filum (Linnaeus) Stackhouse	B, S & I, Sh	Yes
	Alaria esculenta (Linnaeus) Greville	B, S & I, HE	No
	Fucus spiralis (Linnaeus)	B, E, I, Sh	Yes
	Fucus serratus (Linnaeus)	B, E, I, Sh	Yes
	Fucus vesiculosus (Linnaeus)	B, E, I, Sh	Yes
	Ectocarpus siliculosus (Dillynn) Lyngbye	B	Yes
	Lamenaria digitata (Hudson) J.V. Lamouroux	B, E, S & I	No
	Lamenaria hyperborea (Gunnerus) Foslie	B, S & I	No
	Lamenaria saccharina (J.V Lamouroux)	B, S, Sh	No
	Himanthalia elongate (Linnaeus) S.F. Gray	B, E, ME, I & S	No
Annelida	*Pomotoceros triqueter (Linnaeus)*	B, S, E	Yes
	Arenicola marina (Linnaeus)	M, S & I	No
Bryozoa	*Bugula flabellata (Thompson) Gray*	B, S, E	Yes

	Umbonula littoralis Hastings	B, S, E	Yes
	Membranipora menbranacea (Linnaeus)	B, S, E	Yes
Mollusca	*Aplysia puntata (Cuvier)*	M, I & S	No
	Archidoris pseudoargus (Rapp)	M, I & S	No
	Tectura virginea	B, M, E, I	Yes
	Helicon pellucidum (Linnaeus)	B, M, E, S	Yes
	Patella vulgate (Linnaeus)	B, M, S &I	No
Crustacea	*Semibalanus balanoides (Linnaeus)*	B, I	Yes
	Chathamus montagui (Southward)	B, I	Yes
	Balanus crenatus (Brugiere)	B, S, E	Yes
Cnidaria	*Cyanea capillata (Linnaeus)*	P	No
	Actina equine (Linnaeus)	B, E, I, HE, Sh	No
Porphyra	*Halichondria panacea (Pallas)*	B, E, I & S	No
Echinodermata	*Echinus esculentus (Linnaeus)*	B, M, S	No
Chordata	*Botrylloides schlosseri (Pallas)*	E, S & I	Yes
	Botrylloides leachi (Savigny)	E, S & I	Yes

4.2.3 – Experimental Design

The experimental approach was uni-factorial with surface complexity as the main factor. Casts of replica rocks were arranged in a frame constructed of PVC tubing. Frames were cut to size and held together using OSMA solvent cement No. 2. Settlement panels were attached using cable ties in rows of eight with two replicates per row (Fig. 4.6).

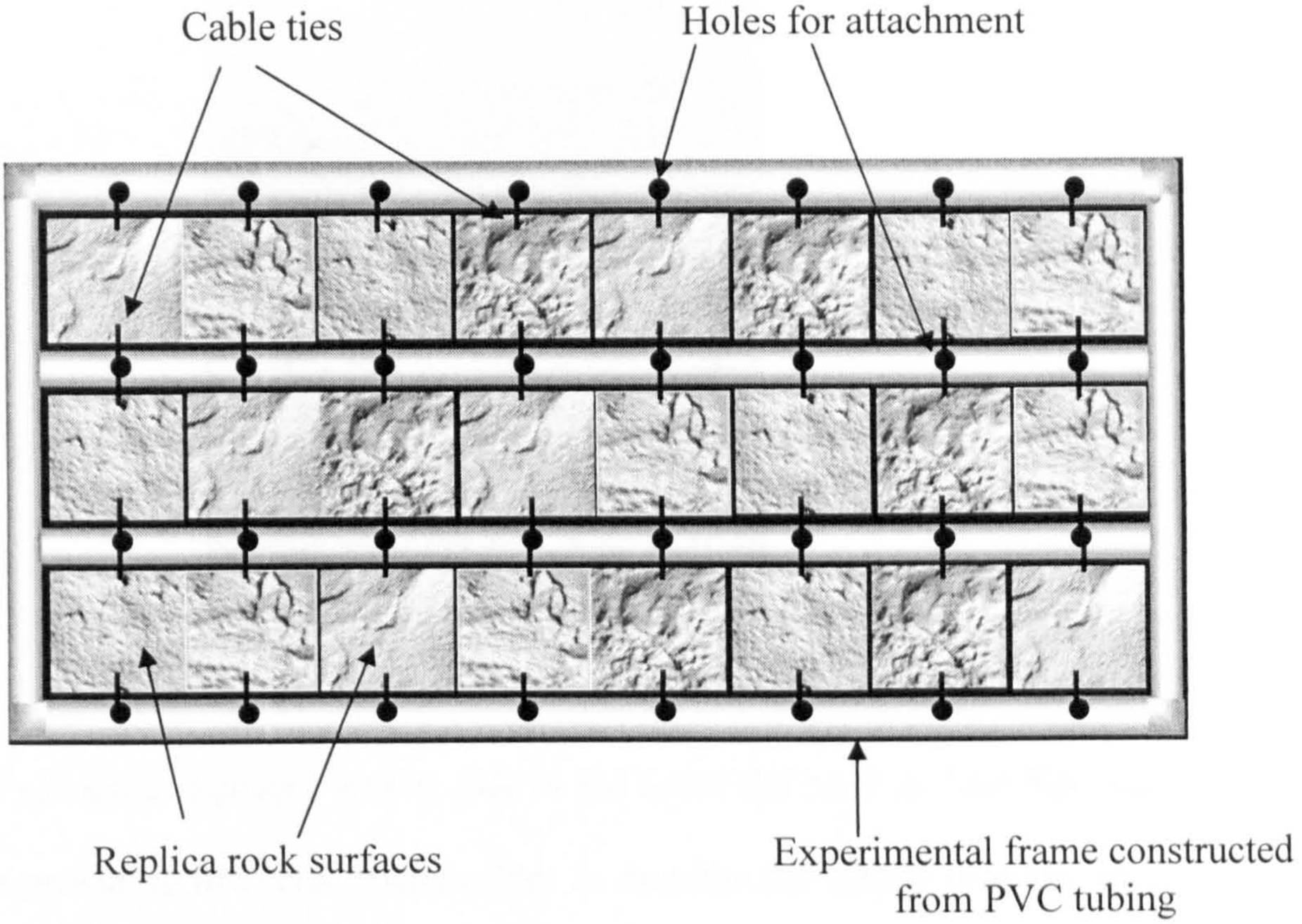


Figure 4.6 – Schematic diagram of the arrangement of settlement panels in experimental frames

4.2.31 – Exposure experiment

In the exposure experiments, frames were fixed to the bedrock at low tide for two months prior to monitoring, to allow for natural colonization. After the initial two months the panels were then monitored to determine the effects of exposure on the communities (Fig. 4.7). A rock drill was used to create holes for attachment and metal rods were used as anchor points. Frames were attached to the metal rods using cable ties.

Figure 4.7 –Frames deployed at low tide in the intertidal zone at Low Newton by the Sea providing artificial communities to monitor the effects of exposure. Frames were attached to metal rods, drilled into the bedrock, using cable ties.

The two frames deployed in the intertidal zone were located at 0.9 m and 1.45 m above chart datum and were referred to as low and high intertidal frames respectively. The exposure times for each frame for the entire experimental period can be seen in Fig. 4.9.

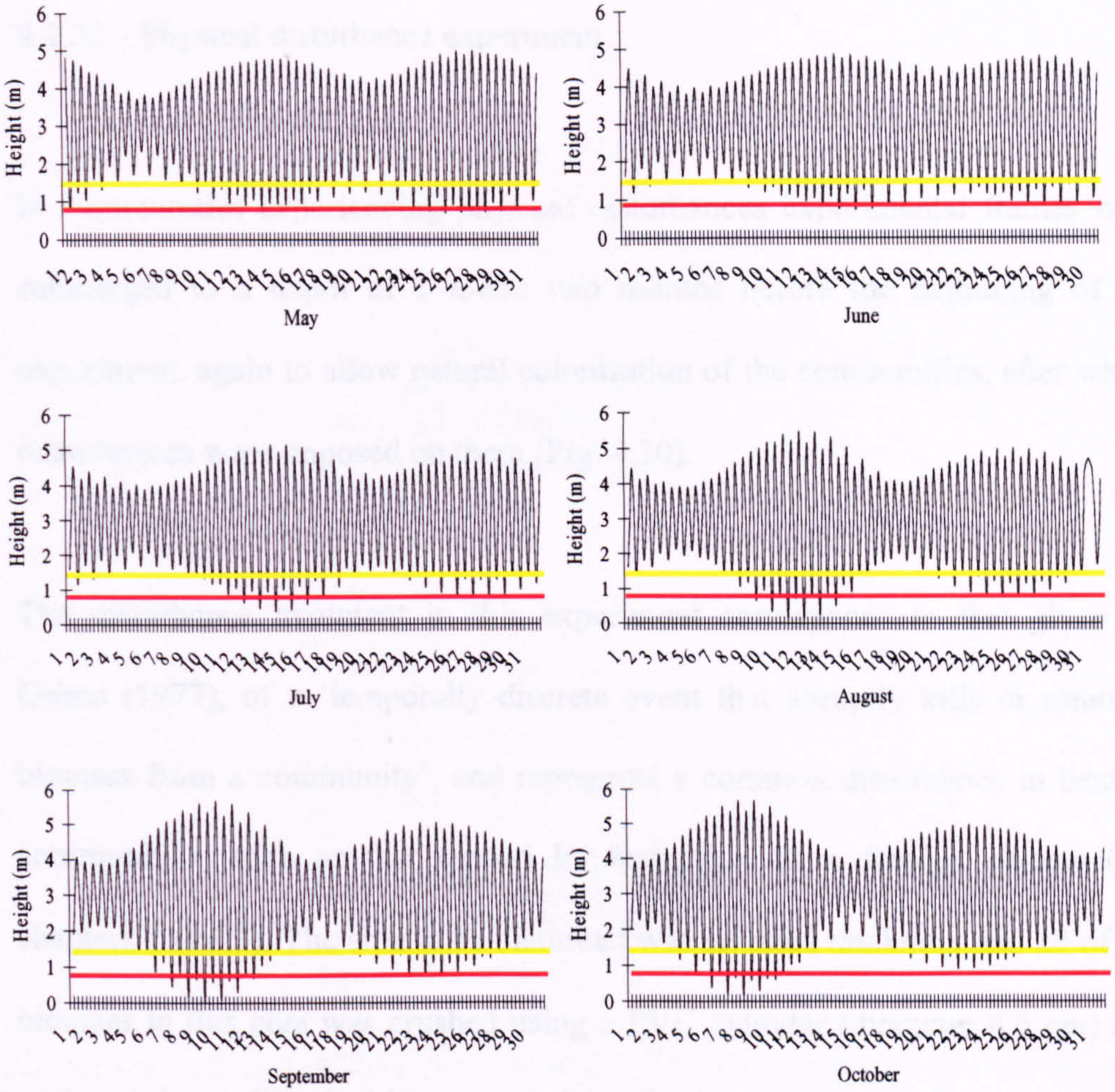


Figure 4.9 – Tidal regime for the six month experimental period, red line represents the location of the low intertidal frame whilst the yellow line represents the position of the high intertidal frame; showing the differences in exposure between the two frames.

4.2.32 – Physical disturbance experiment

In communities experiencing physical disturbances experimental frames were submerged to a depth of 1 metre two months before the beginning of the experiment, again to allow natural colonisation of the communities, after which disturbances were imposed on them (Fig. 4.10).

The disturbance treatment in this experiment corresponds to that given by Grime (1977), of a 'temporally discrete event that abruptly kills or removes biomass from a community', and represents a common disturbance in benthic communities, such as that caused by impaction from foreign objects (see chapters 2 and 3). The area to be disturbed was selected randomly and all of the biomass in this area was crushed using a PVC cylinder (diameter 4.6 cm) and each panel was disturbed in one area. Disturbances were applied every 6 weeks, (Fig. 4.11) and this frequency of disturbance was chosen due to the results found in chapter one which indicated that subtidal benthic communities appeared to survive with high level of diversity when disturbances occurred at this frequency. Communities were returned to the moorings after disturbances.

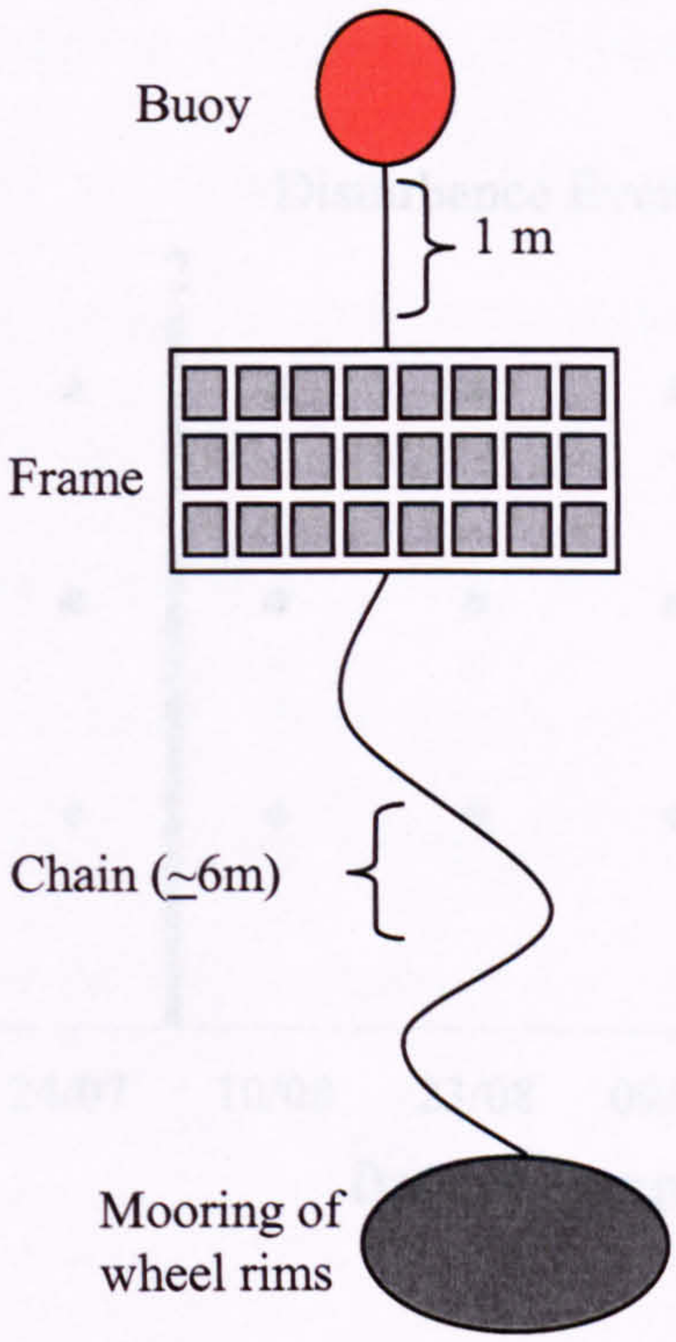


Figure 4.10 – Schematic diagram illustrating the set up of experimental frames in the subtidal zone for the physical disturbance and hydrodynamic shear experiments.

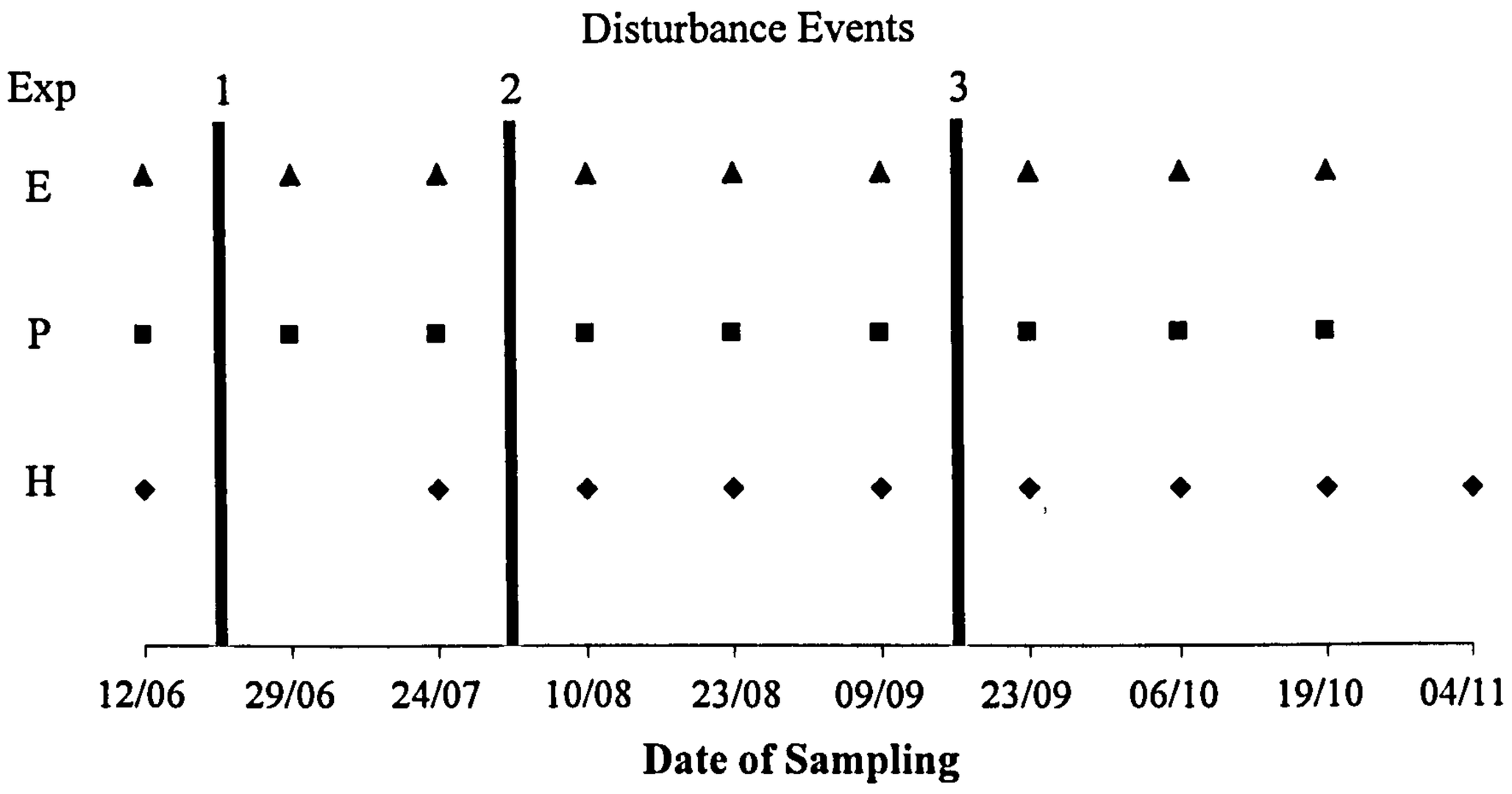


Figure 4.11 – Sampling and disturbance calendar. Symbols represent sampling events and lines represent both physical disturbance and hydrodynamic shear disturbance events. Triangles are the exposure experiments (E) while squares and triangles are the physical disturbance (P) and hydrodynamic shear experiments (H) respectively. Missing squares indicate that sampling on this day for a particular experiment was not possible due to adverse weather conditions.

4.2.33 – Hydrodynamic shear experiment

In communities experiencing hydrodynamic shear experimental frames were deployed in the same way as those undergoing physical disturbances (Fig. 4.10).

The disturbance treatment applied to the communities corresponds to that of heavy wave action such as occurs when a severe storm hits the coastline. A water jet (Fig. 4.12) designed by Swain & Scultz (1996) for testing the adhesion potential of fouling organisms, was used to periodically manipulate the hydrodynamic shear imposed onto the subtidal community. The water jet worked using a SCUBA tank of compressed air to pump the water out at a pressure of 13.8 kPa through a pressure gun and onto the communities. The frequency of hydrodynamic shear events was the same as in the physical disturbance experiments, every 6 weeks. Communities were disturbed for approximately 2 minutes. Communities were returned to the moorings after disturbance events.

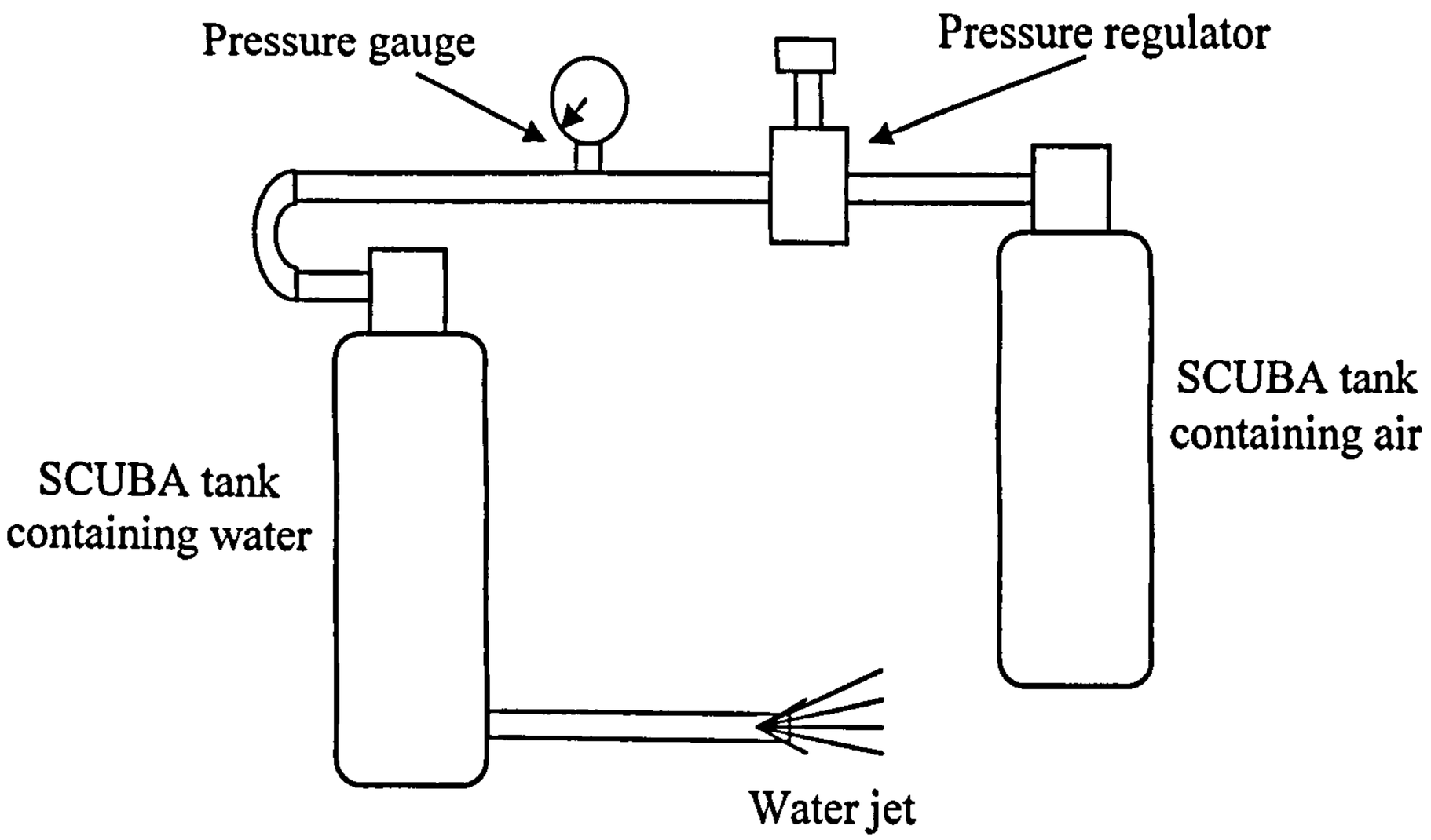


Figure 4.12 – Schematic diagram illustrating the water jet used to create hydrodynamic shear (after Swain & Schultz 1996).

4.2.4 - Sampling

The sampling of communities was carried out in the same way as in previous chapters (see chapter 2 and 3). Whilst estimating the percentage cover of each species the xy coordinates for the location of each individual within each species was also recorded using the sampling grid shown in Fig. 4.2 and ImageJ cell counter. A 1 cm edge was left unsampled to avoid the sampling of edge effects. Species identification was verified in the field.

4.2.5 - Data Analysis

Species abundances were measured and used to calculate the total abundance of the experimental communities as well as the diversity parameters Shannon index (H'), Piloeu's Evenness and species richness (Magurran 1988). All indices were then analysed with a repeated measures ANOVA testing for the effects of surface complexity over the experimental period following the linear model:

$$X_{ijk} = \mu + S_i + T_k + ST_{ik} + e_{j(ik)}$$

Where X_{ijk} represent the data in plot *j*, in treatment *i* at time *k*. S and T represent the effects of surface complexity, if they exist, and time of sampling while the interaction, if present, is represented by ST; $e_{j(ik)}$ represents the *jth* replicate plot

sampled in treatment *i* at time *k*, as well as any source of variation in X_{ijk} that is not accounted for by the other terms in the model (Underwood 1997).

Multivariate analysis was then done on the species abundances in order to determine not only whether the diversity of the communities changed over time but also whether the composition of the communities changed over time. PRC analysis simplifies the presentation of such time-based analyses by plotting the differences in community composition for each treatment relative to a baseline treatment (considered as a control: R1) against time. In PRC the basic model (following the syntax of Van den Brink & Ter Braak 1999) is:

$$Y_{d(j)tk} = Y_{0tk} + b_k c_{dt} + e_{d(j)tk}$$

Where $Y_{d(j)tk}$ is the abundance of species *k* in replicate *j* of treatment *d* at time *t*; Y_{0tk} is the mean abundance of species k at time t in the control ($d = 0$); b_k is the weight of each species, fitted to the basic response c_{dt}; $e_{d(j)tk}$ is an error term with zero mean and σ^2_k variance. Note that $c_{0t} = 0$ for every *t* and *k*. The partial least-squares estimates of the coefficients (c_{dt}) can be determined through partial redundancy analysis (RDA), and the c_{dt} values plotted as PRC axis 1 (on the y-axis) against sampling time (x-axis) for each treatment. The resulting curves for each treatment show the principal community response over time, in comparison with the baseline treatment. The species weights (b_k) show how closely each species matched the overall community change with time, and can also be plotted on the PRC graph. The significance of the PRC can be tested via

a Monte Carlo permutation test of the samples (i.e. permuting whole time-series) in the partial RDA used to develop the PRC.

An analysis of cross classifications using cross tabulations was then performed to examine the relationship of species settlement to the availability of refuges within a level of surface complexity, as an independent test for the measure of association between the data. This permits an examination of the frequency of settlement of each species within a type of refuge, and details the significance of this settlement in relation to that expected by chance.

4.3 – Results

The natural sessile benthic community at Low Newton by the Sea was comprised of 31 species with the majority of available space for settlement being occupied by large macroalgae such as kelps and fucoids. The mobile organisms in this area were comprised from 7 phyla with numerous species per phylum, resulting in an area of high biodiversity (Table 4.6) in comparison with the other experimental areas of Hartlepool and Sunderland.

4.3.1 – Intertidal Exposure experiments

Repeated measures ANOVA showed significant changes in species diversity (H'), evenness and richness overtime in the intertidal desiccation experiments, at both levels of exposure, highlighting the temporal recruitment of species into the communities. In communities located on the lower shore, and therefore exposed for less time, surface complexity had a strong significant effect on diversity (H'), evenness and species richness. At this shore height habitat complexity also significantly interacted with time for each of these variables. Interestingly this was not the case in the communities exposed for longer, those higher up the shore. In this case there were only significant effects of time (Table 4.7, Fig. 4.13). In both cases the significant effects of time can clearly be seen in the succession of the communities (Figs. 4.14 & 4.15), with the more complex surfaces having a greater cover of species as well as a greater number of species much earlier on than the less complex surfaces.

Table 4.7 – Repeated measures ANOVA for communities experiencing low and high levels of exposure. Significant values are highlighted in grey where; SS = type III sums of squares, df = degrees of freedom, MS = mean sums of squares, F =F-value, P = probability of significance α <0.05.

Dependant Variable	Source of Variation	Low Desiccation SS	df	MS	F	P	High Desiccation SS	df	MS	F	P
Shannon index (H')	Time	7.988	8	0.988	17.829	<0.001	4.278	4.809	0.890	6.0	<0.001
	Time x Surface complexity	3.696	24	0.154	2.750	<0.001	2.454	14.426	0.170	1.147	0.328
	Surface complexity	2.051	3	0.684	5.312	0.007	1.964	3	0.655	0.901	0.458
Species Richness	Time	164.343	5.108	32.171	34.002	<0.001	66.509	4.345	15.307	10.332	<0.001
	Time x Surface complexity	21.657	15.325	1.413	1.494	0.120	17.194	13.035	1.319	0.890	0.566
	Surface complexity	4.718	3	1.573	1.560	0.230	4.014	3	1.338	0.145	0.931
Evenness	Time	0.575	3.045	0.189	2.010	0.121	1.010	4.223	0.239	1.915	0.112
	Time x Surface complexity	2.008	9.136	0.220	2.342	0.024	1.722	12.670	0.136	1.089	0.380
	Surface complexity	1.677	3	0.559	10.874	<0.001	1.702	3	0.567	2.292	0.109
Total Abundance	Time	104320.444	3.063	34060.884	44.556	<0.001	32455.942	1.775	18288.025	16.864	<0.001
	Time x Surface complexity	14460.852	9.188	1573.835	2.059	0.046	6128.193	5.324	1151.022	1.061	0.400
	Surface complexity	33555.747	3	11185.249	3.484	0.035	14789.273	3	4929.758	1.095	0.374

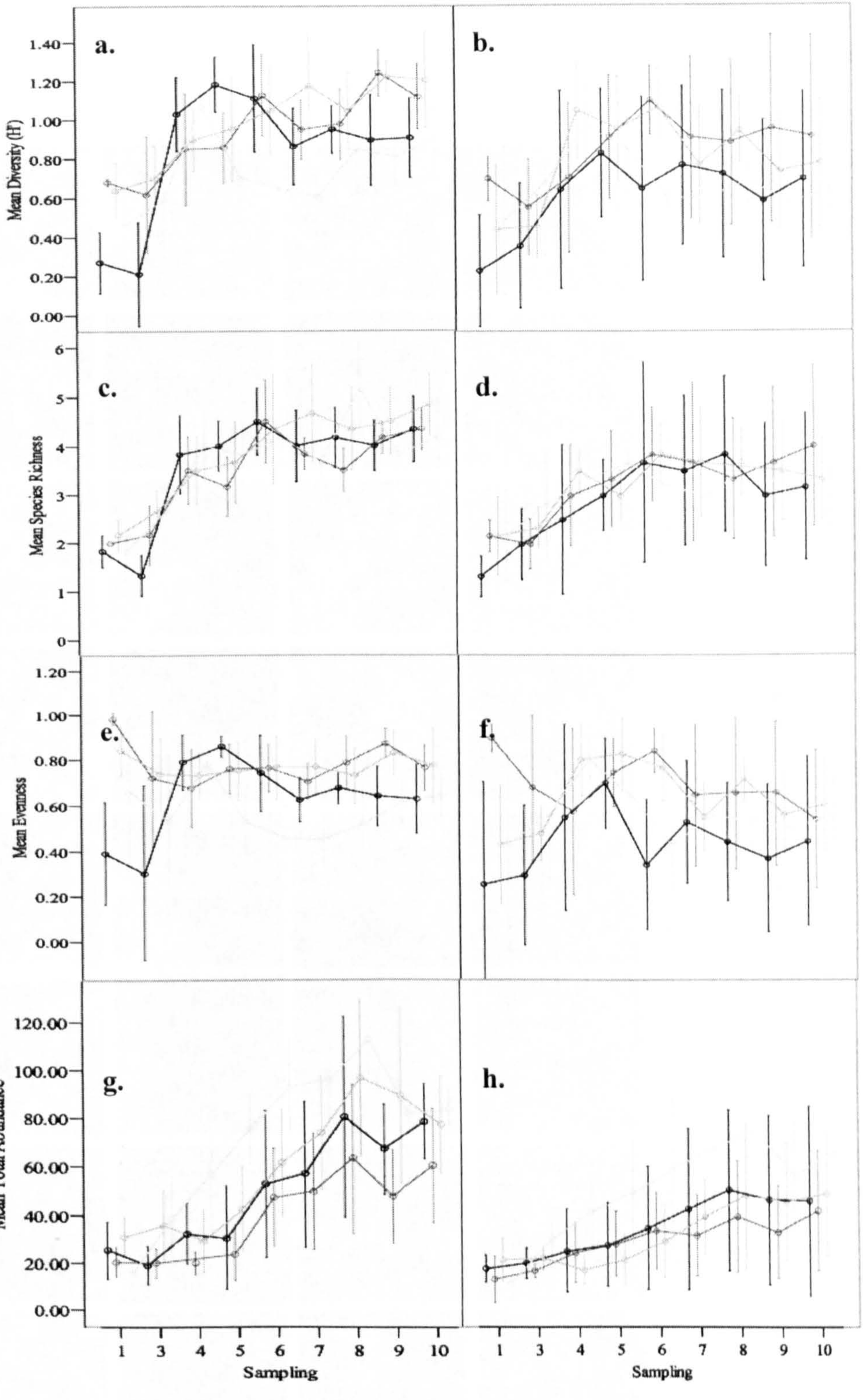


Figure 4.13 – Mean (± SE) diversity (H'), species richness, evenness and total abundance for communities subjected to low (a, c, e, g) and high (b, d, f, h) levels of exposure on the different levels of surface complexity: R1 - ▬, R2 - ▬, R3 - ▬, R4 – ▬ (n = 6 per treatment, per sampling).

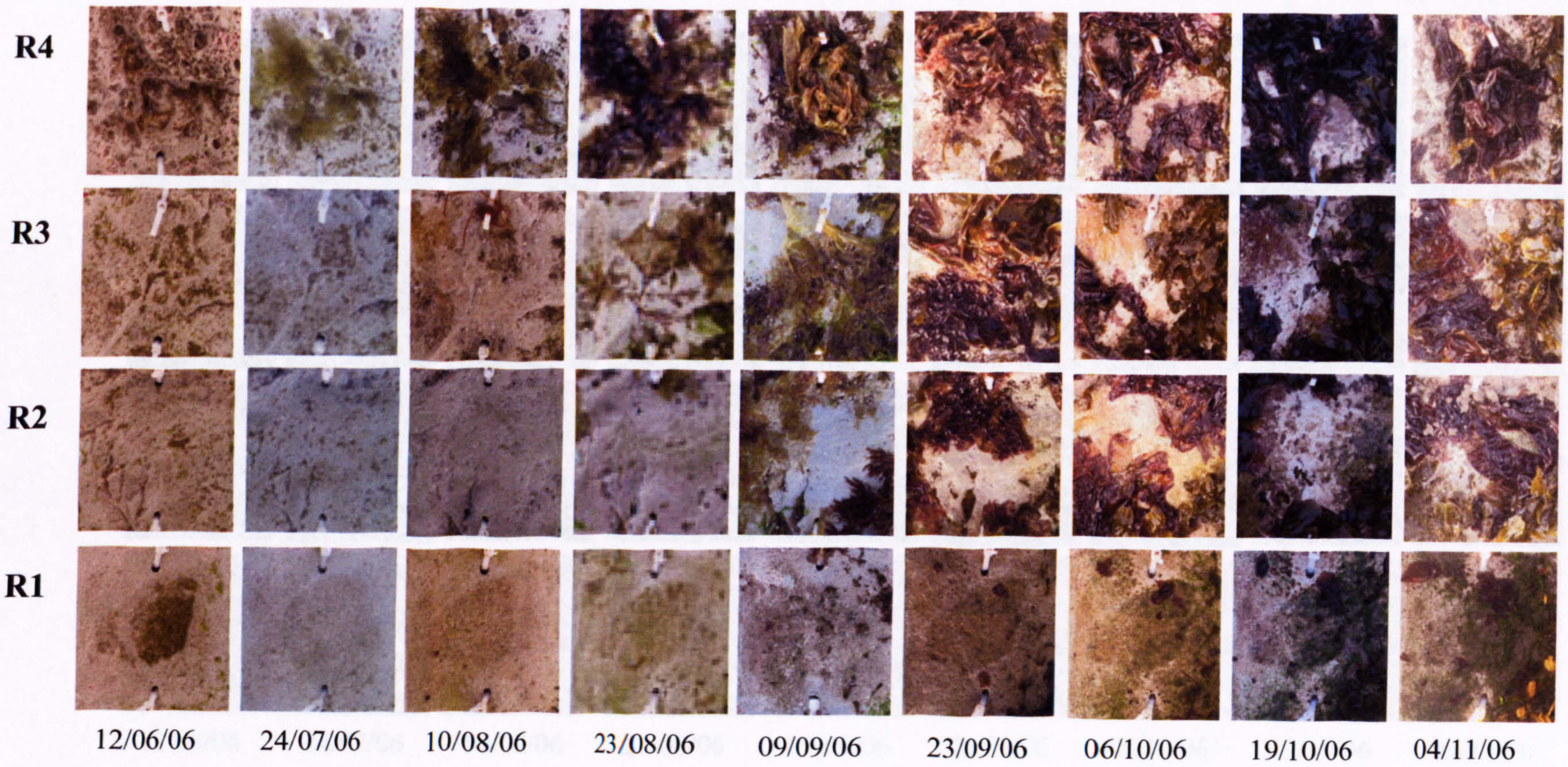


Figure 4.14 – Development of communities at the low exposure level over the nine sampling dates on the four levels of surface complexity: R1, R2, R3, R4

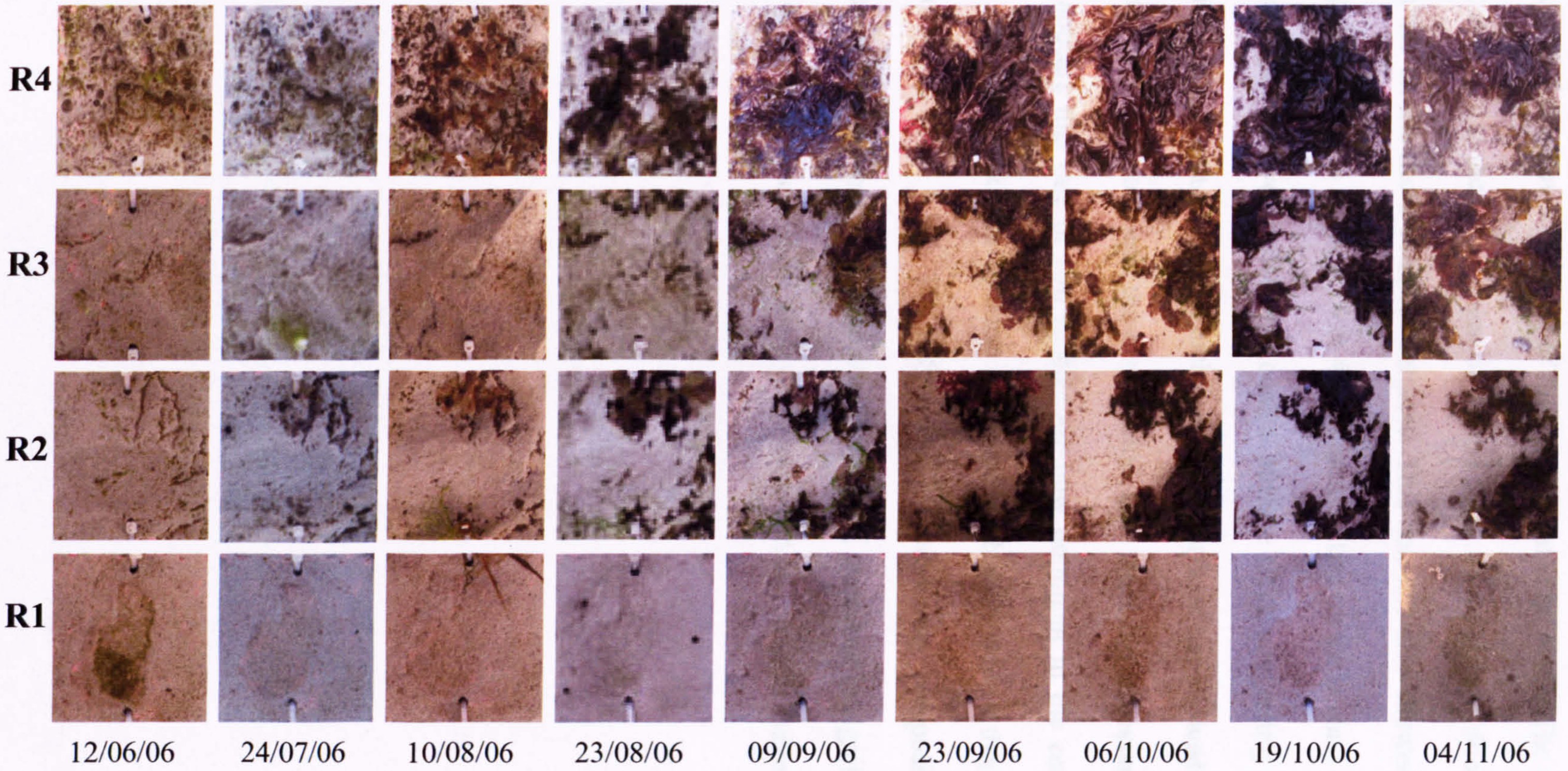
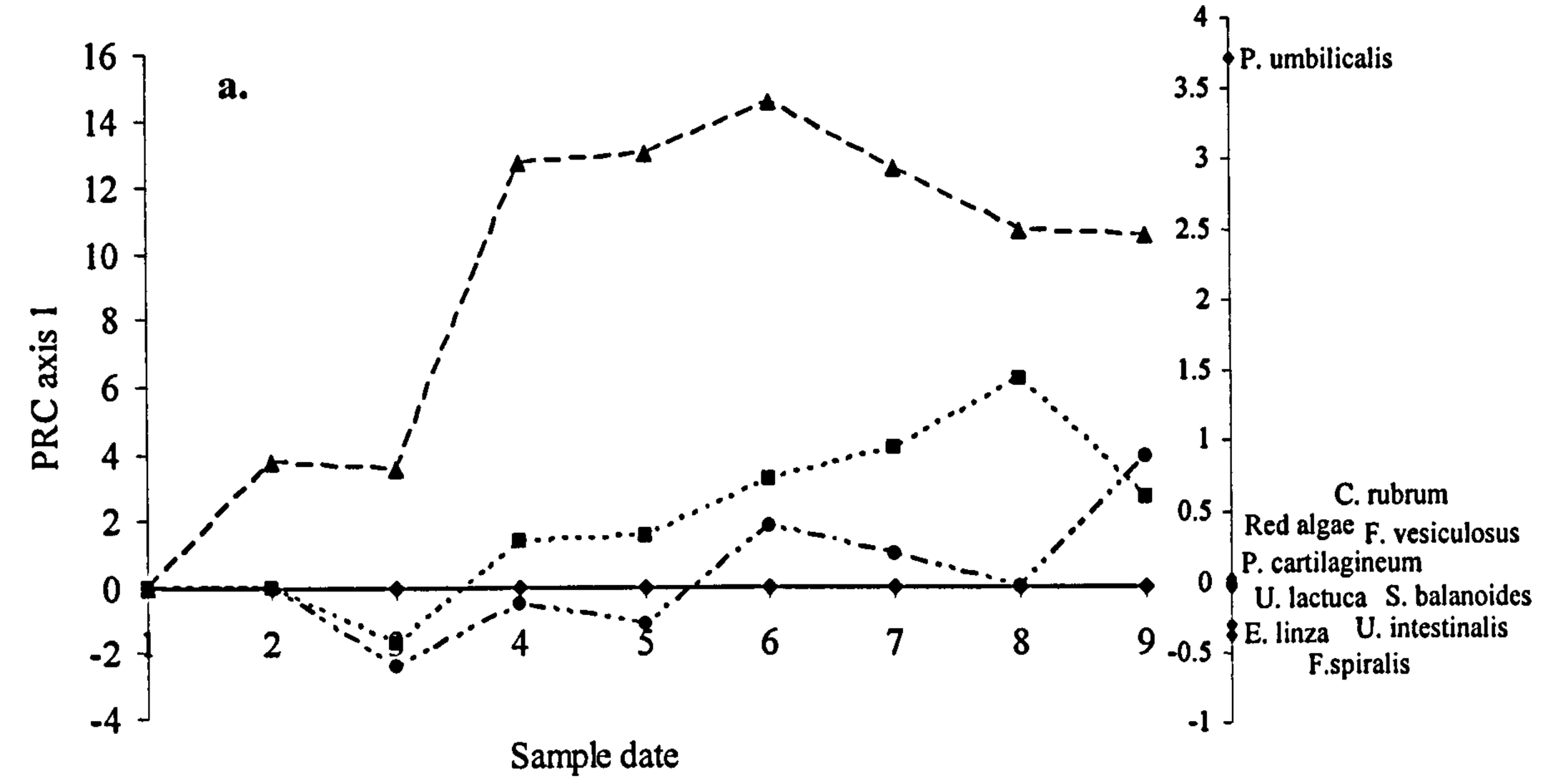


Figure 4.15 - Development of communities at the high exposure level over the nine sampling dates on the four levels of surface complexity: R1, R2, R3, R4

PRC showed that at both levels of exposure the communities on the most complex surfaces diverged from the less complex surfaces from the onset of the experiment, and these differences increased over the time of the experiment (Fig. 4.16). The communities differed, in both cases, due to the contribution of the red algae; *Porphyra umbilicalis*, which dominated communities on the more complex surfaces. This analysis also showed that from the fourth sampling date onwards (Figs. 4.14 & 4.15) communities on the second most complex surface (R3) also began to diverge from the control surface (R1), suggesting that the settlement of mainly algae into the the structural niches on these surfaces has allowed them a foothold from which they can grow out into the community. This does not necessarily increase diversity since it appears that one or two species are now dominant in the community, but it does increase the total abundance of these communities directly due to this dominance by a few species of algae (Fig. 4.13). The differences in community composition on the different surface complexities, seen at both levels of exposure, were highly significant ($P = 0.002$) and the species scores accounting for these differences can be found in Table 4.8.



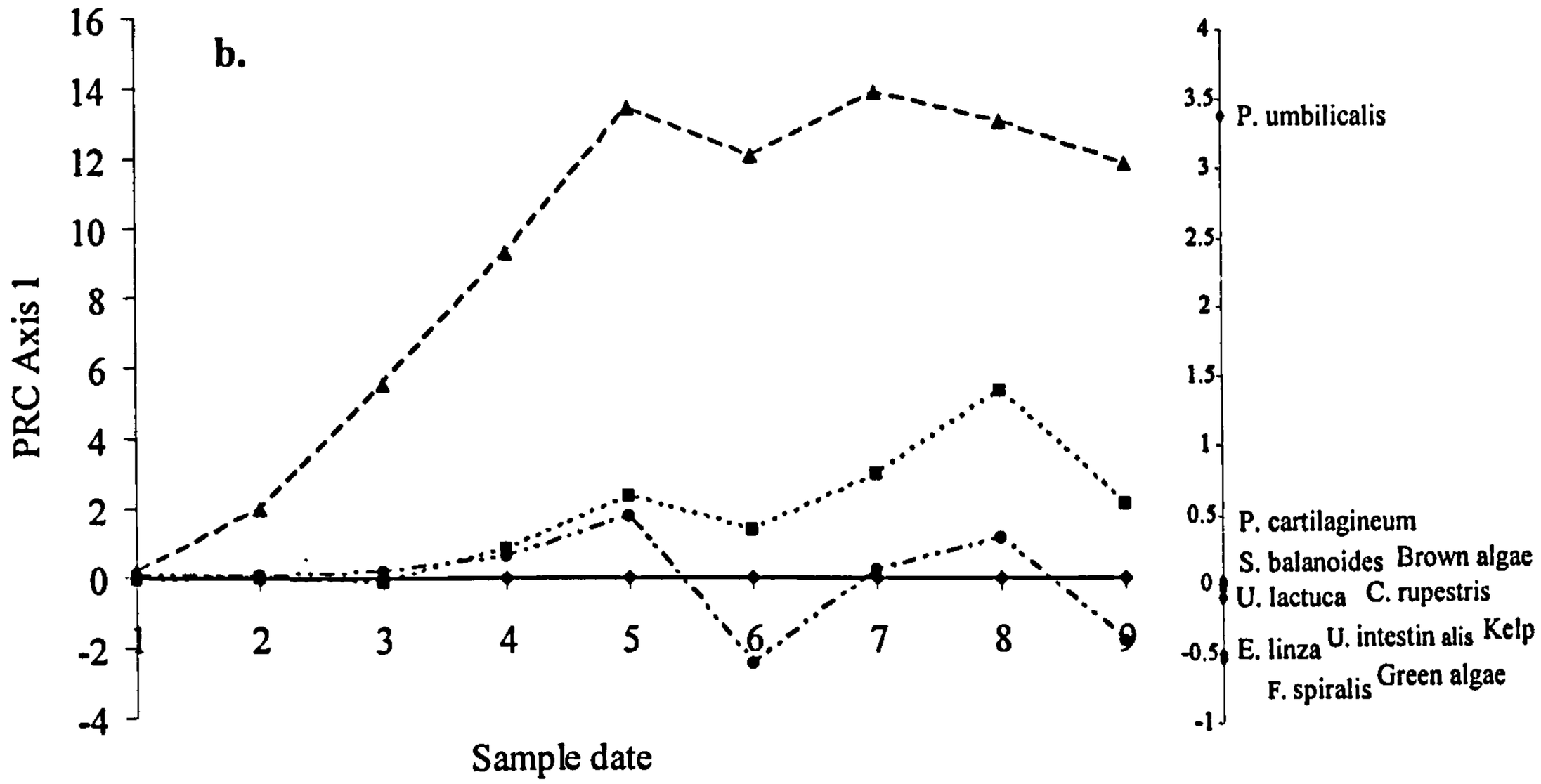


Figure 4.16 – Principal response curve for communities at a. low exposure level and b. high exposure level where: R1 -◆- , R2 -●- , R3 -■- , R4 -▲- . Monte Carlo test for significance at the low exposure level: eigen-value = 0.192, F ratio = 74.699, P-value = 0.0020, and the high exposure level: eigen-value = 0.253, F ratio = 78.444, P-value = 0.0020.

Table 4.8 – Species scores comprising the principal components analysis for communities at low and high levels of exposure

Species Name	Species Scores	
	Low Desiccation	High Desiccation
Plocamium cartilagineum	-0.0283	0.0217
Porphyra umbilicalis	3.7103	3.3797
Ulva lactuca	-0.0041	-0.0169
Ulva intestinalis	-0.014	-0.0408
Enteromorpha linza	-0.3007	-0.5031
Fucus	-0.3741	-0.5512
Semibalanus balanoides	-0.0072	0.0028
Green filamentous algae	-0.0083	-0.1018
Brown filamentous algae	0.0378	-0.0878
Petalonia fascia	-0.0159	-0.0115
Patella vulgata	-	-0.0015
Kelp	-	-0.004
Cladophora rupestris	0.0062	-
Ceramium rubrum	0.0099	-
Red filamentous algae	0.0006	-
Fucus vesiculosus	-0.0058	-

The relative distribution of each of the dominant species in these communities in relation to the different structural niches found on each of the different surface complexities was examined. It can very clearly be seen that a higher percentage of spores or larvae from these species settled in the more complex niches and expanded outwards from these positions, at both levels of exposure, on all levels of surface complexity (Tables 4.9a-d). This relationship is very strong and highly significant (Chi-square 0.3, $P<0.001$), and is by caused by the occurrence of 'hilly' refuges and the settlement of Fucus spp, *Semibalanus balanoides* and *Porphyra umbilicalis* on the control surfaces (R1). Although this relationship is observed on the three levels of surface complexity (R2, R3, R4) the result was not significant indicating that the high level of settlement of a species in a particular structural niche can be explained by chance. There were no significant relationships between any species and any structural niche on any level of surface complexity in communities experiencing higher levels of exposure.

Table 4.9a – Percentage occurrence of species on each of the structural niches available for settlement on smooth panels in the low (L) and high (H) desiccation experiment where: ● *- >70 %* ● *- 61-70%* ● *- 51-60 %* ● *- 41-50 %* • *- 31-40 %* • *- 21-30 %* • *- 11-20 %* · *- 0-10 %*

Refuge	Fucus Spp		*S. balanoides*		*P. umbilicalis*		Green algae		*U. lactuca*		*U. intestinalis*		*E. linza*		*P. cartilagineum*		*E. siliculosus*		*P. palmata*		Brown algae	
Experiment	L	H	L	H	L	H	L	H	L	H	L	H	L	H	L	H	L	H	L	H	L	H
Double incline & ledge																						
Steep incline & crevice																						
Steep Incline & Peak																						
Steep incline & Ledge																						
Crevice & Peak																						
Medium Hill																						
Peak																						
Crevice																						
Step up crevice & peak																						
Steep incline																						
Medium ledge & incline																						
Uphill flat base																						
Uphill to peak																						
Hill																						
Incline																						
Ledge & Slope	•	·	•	•	●	·	•			·		·	•	•		·						
Bowl	●	·	•	•	●	·								•							•	
Shallow Pit	•	·	·	•	•	·	•		·	·			·	·		·						
Gentle Peak	•	•	•	•	•		·		·					·								
Slope	·	·	•	•	•	·	·		·		·		·	·		·					·	
Hilly	•	·	·	·	•		·		·		·	·	·	•		·				·	·	
Flat	•	·	·	·	•	·	·		·		·	·		•		·				·		

Table 4.9b – Percentage occurrence of species on each of the structural niches available for settlement on R1 panels in the low (L) and high (H) desiccation experiment where: ● *- >70 %* ● *- 61-70%* ● *- 51-60 %* ● *- 41-50 %* • *- 31-40 %* • *- 21-30 %* • *- 11-20 %* · *- 0-10 %*

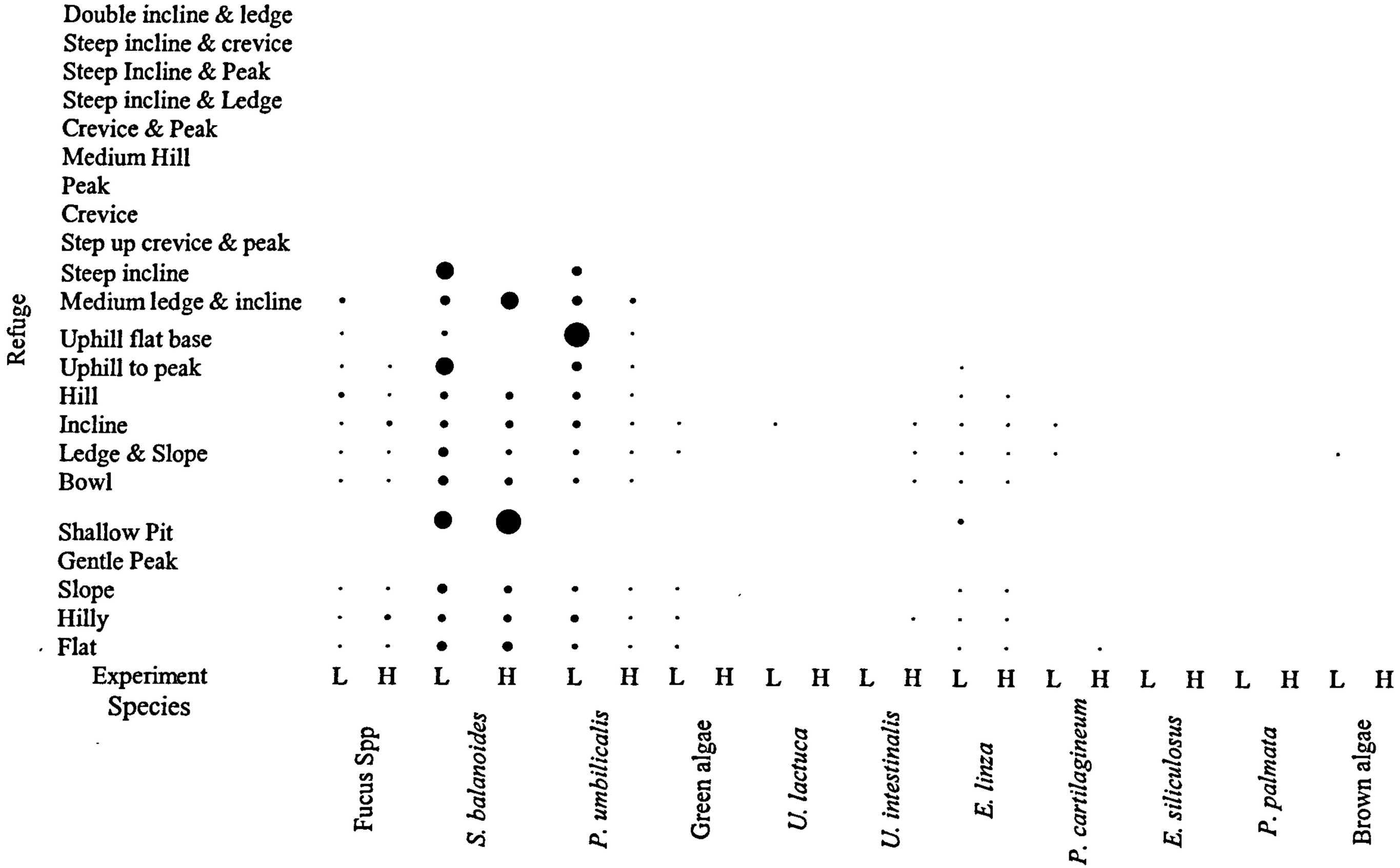


Table 4.9c – Percentage occurrence of species on each of the structural niches available for settlement on R2 panels in the low (L) and high (H) desiccation experiment where: ● *- >70 %* ● *- 61-70%* ● *- 51-60 %* ● *- 41-50 %* • *- 31-40 %* • *- 21-30 %* · *- 11-20 %* · *- 0-10 %*

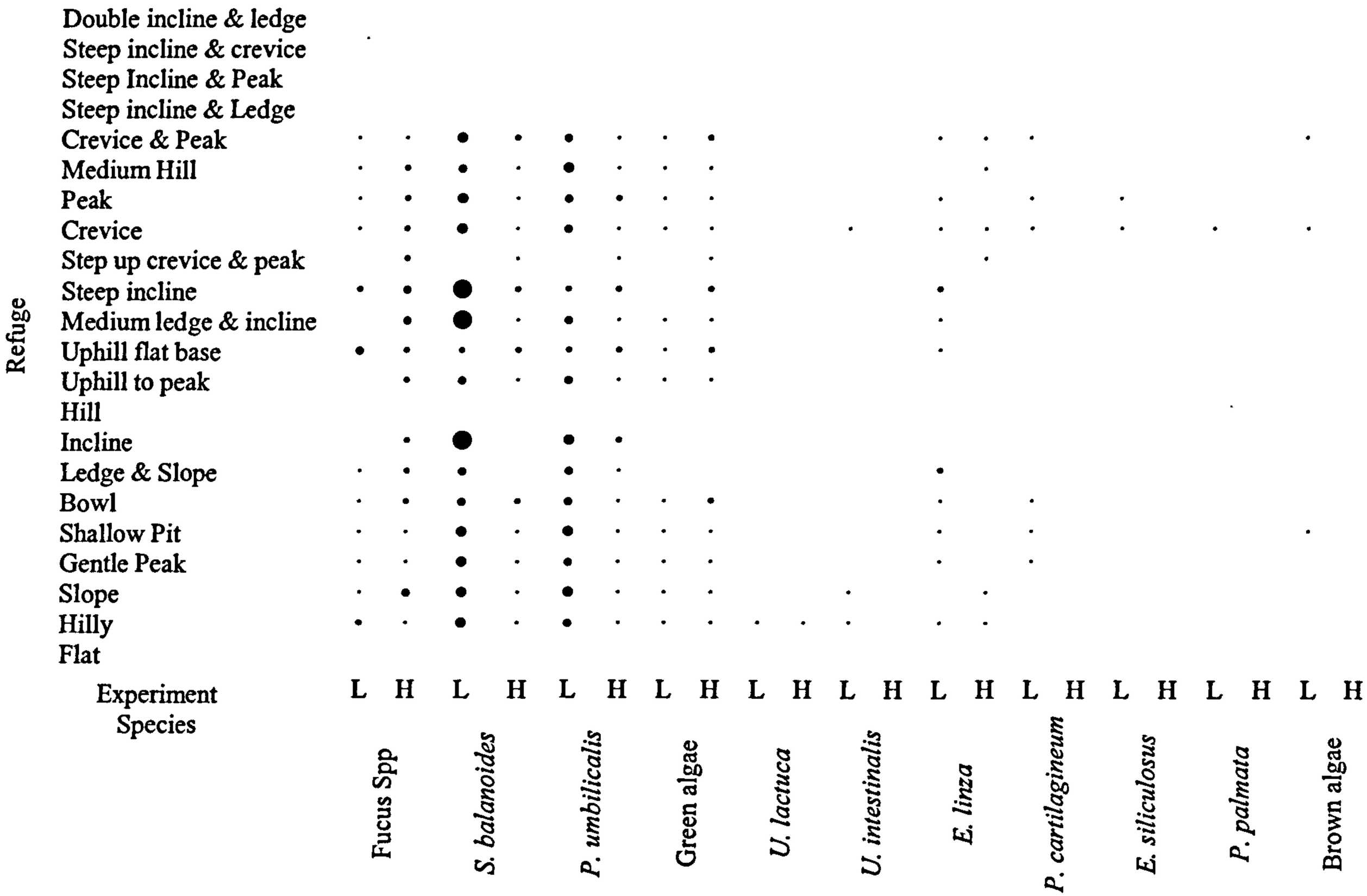
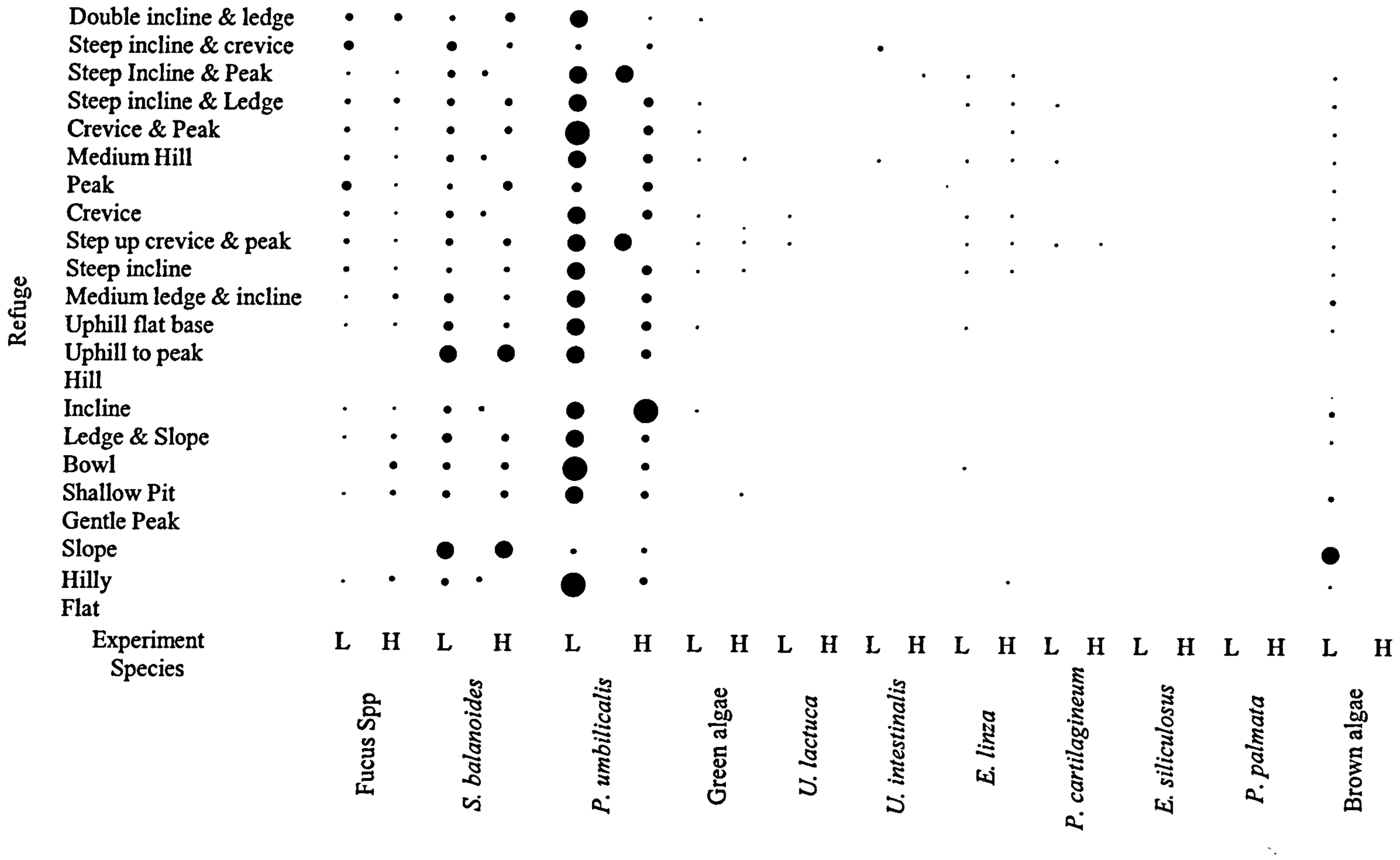


Table 4.9d – Percentage occurrence of species on each of the structural niches available for settlement on R3 panels in the low (L) and high (H) desiccation experiment where: ● *- >70 %* ● *- 61-70%* ● *- 51-60 %* ● *- 41-50 %* • *- 31-40 %* • *- 21-30 %* • *- 11-20 %* · *- 0-10 %*



4.3.2 – Physical disturbance experiment

Repeated measures ANOVA showed that there were always significant effects of time, on all diversity parameters measured, in the subtidal communities undergoing physical disturbance. There were no significant effects of surface complexity or interactions between surface complexity and time (Table 4.9, Fig. 4.17). Despite this a very clear pattern could be seen in the succession of these communities over time with differences in community composition appearing between levels of surface complexity (Fig 4.18).

Table 4.9 – Repeated measures ANOVA for communities experiencing physical disturbances. Significant values are highlighted in grey where: SS = type III sums of squares, df = degrees of freedom, MS = mean sums of squares, F =F-value, P =probability of significance at α <0.05.

Dependant Variable	Source of Variation	Physical Disturbance				
		SS	df	MS	F	P
Shannon index (H')	Time	18.142	4.743	3.825	42.365	≤0.001
	Time x surface complexity	0.955	14.299	0.067	0.744	0.727
	Surface complexity	0.336	3.000	0.112	0.863	0.477
Species Richness	Time	1015.820	4.623	219.728	81.926	≤0.001
	Time x surface complexity	23.304	13.869	1.680	0.626	0.835
	Surface complexity	3.198	3.000	1.066	0.315	0.815
Evenness	Time	3.182	4.154	0.766	22.940	<0.001
	Time x surface complexity	0.4755	12.461	0.038	1.142	0.339
	Surface complexity	0.040	3.000	0.013	0.399	0.756
Total Abundance	Time	29454.599	4.316	6823.884	53.001	≤0.001
	Time x surface complexity	1502.202	12.949	116.007	0.901	0.555
	Surface complexity	1089.986	3.000	363.329	2.790	0.069

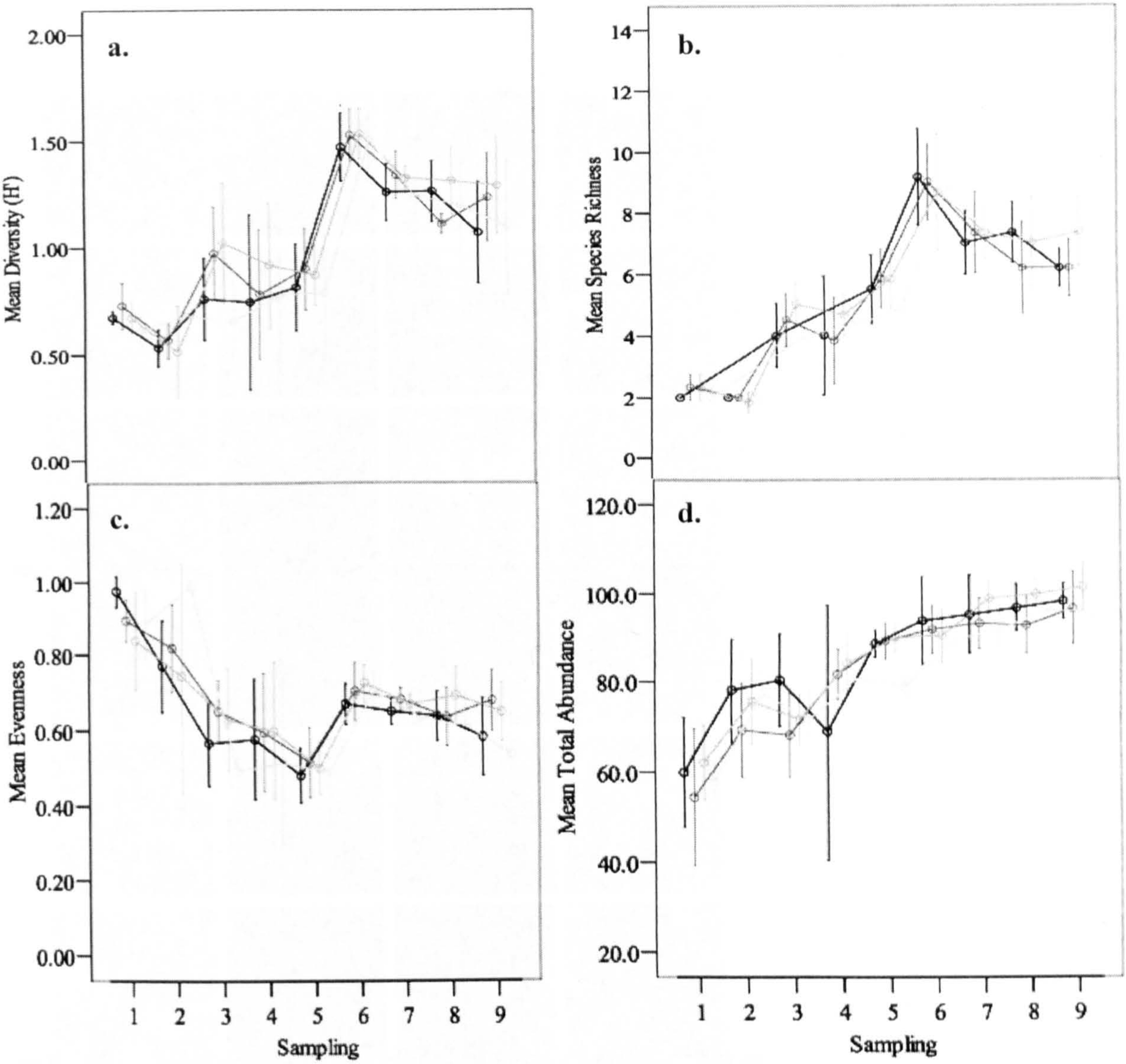


Figure 4.17 – Mean (± SE) a. diversity (H'), b. species richness, c. evenness and d. total abundance for communities subjected to physical disturbances on the different levels of surface complexity: R1 - ▬ , R2 - ▬ , R3 - ▬ , R4 – ▬ (n = 6 per treatment, per sampling).

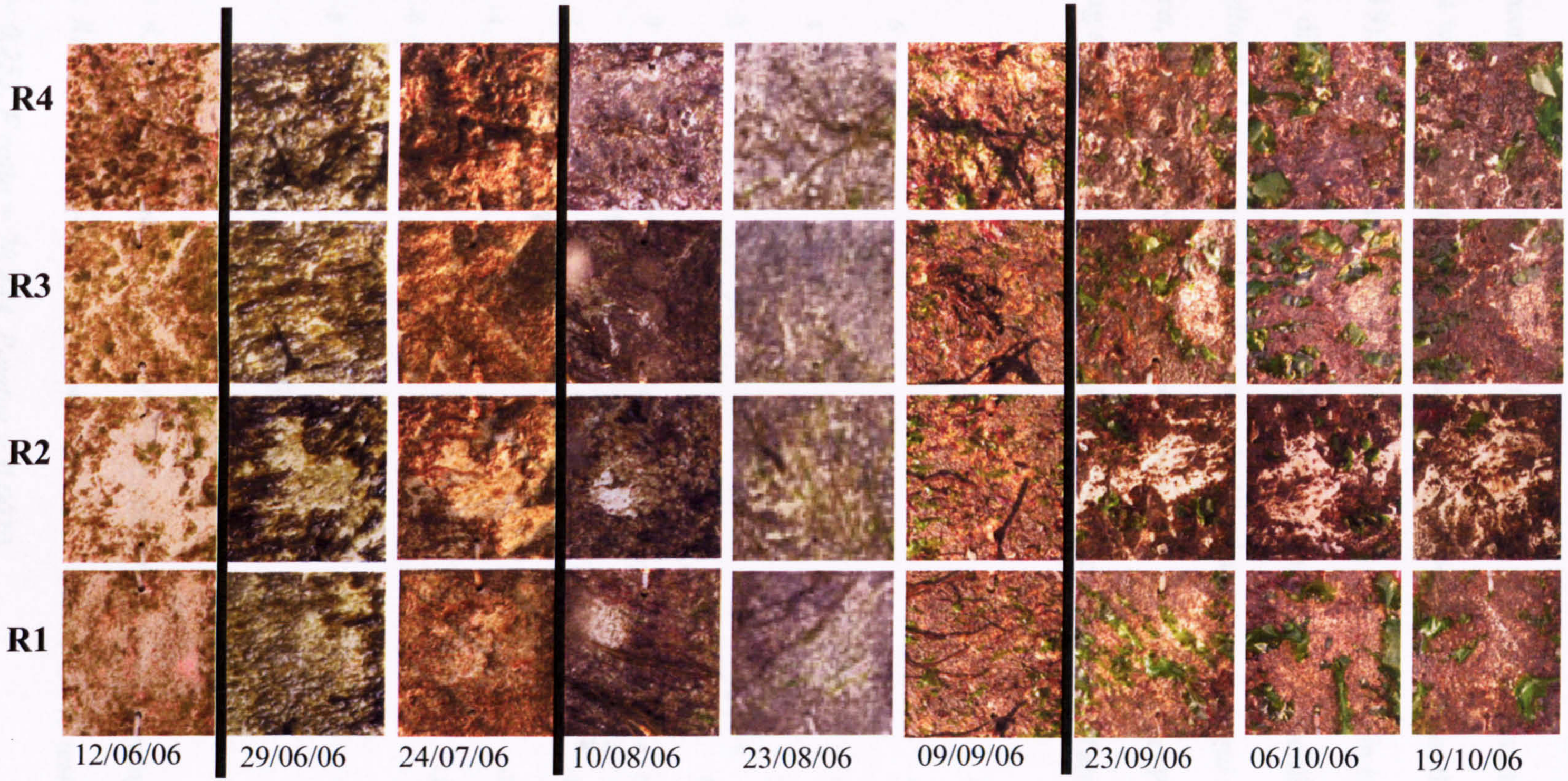


Figure 4.18 - Development of communities experiencing physical disturbances over the nine sampling dates on the four levels of surface complexity: R1, R2, R3, R4, black lines represent disturbance events.

PRC showed that in communities subjected to physical disturbances there are no differences between the community compositions on the different levels of surface complexity for the majority of the experiment. It was only towards the end of the experiment that the communities on the more complex surfaces begin to diverge from the less complex surfaces, and it was due to the presence of brown filamentous algae within the community (Figs. 4.18 & 4.19). The two intermediate complexities (R2 & R3) also begin to diverge at this point but these differences are due to the presence of the colonial ascidians *Didemnum* spp and *Botrylloides leachi*, as well as the barnacle *Chathamalus montagui* and the green algae *Ulva lactuca*, within the community. These effects were not significant (P = 0.712) and the species scoring accounting for the observed divergences can be found in Table 4.11.

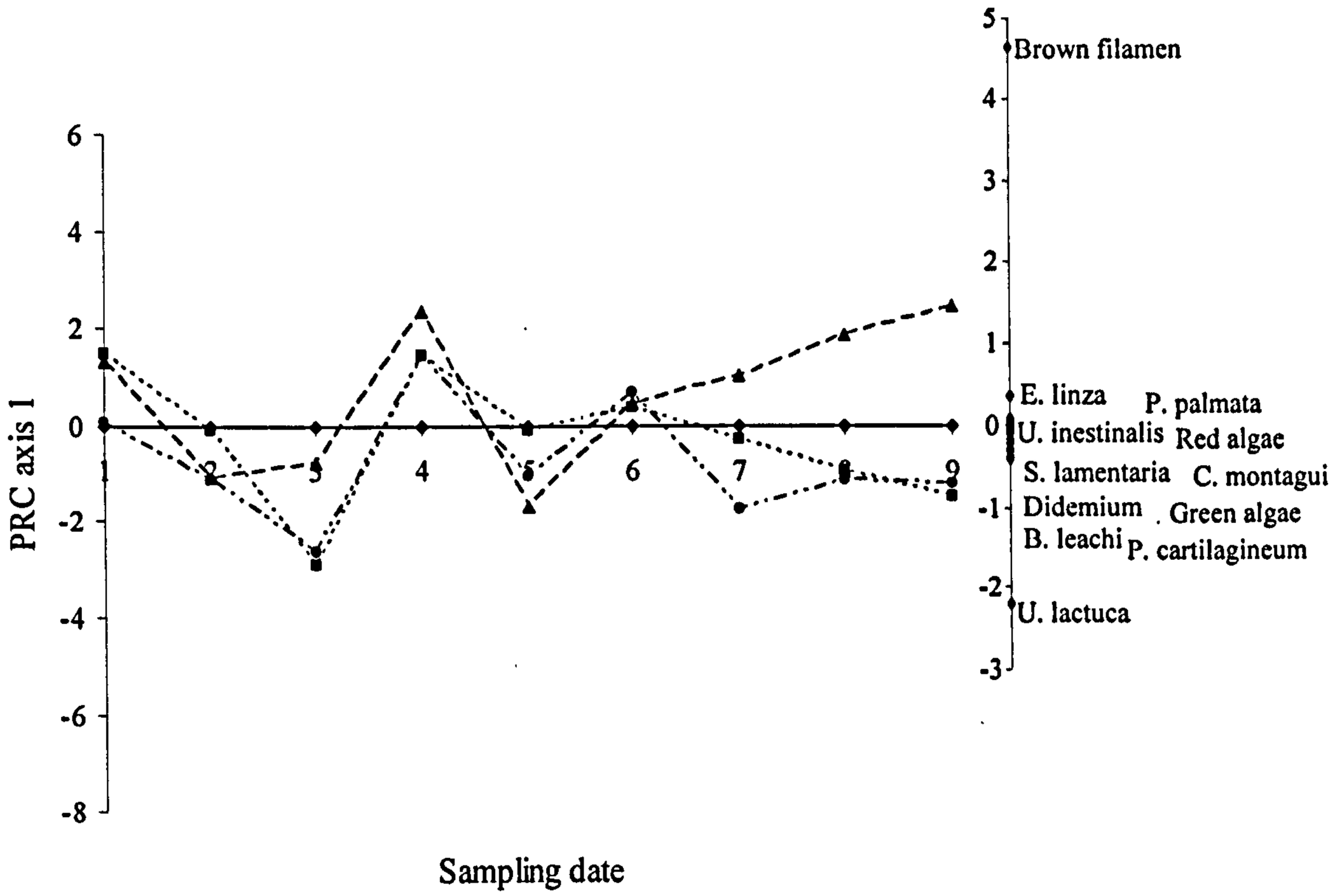


Figure 4.19 - Principal response curve for communities undergoing physical disturbances where: R1 - —◆—, R2 - –●– , R3 - ···■···, R4 - -▲-. Monte Carlo test for significance: eigen-value = 0.253, F ratio = 78.444, P-value = 0.0020.

Table 4.11 - Species scores comprising the principal components analysis for communities undergoing physical disturbances

Species Names	Species Scores
Ulva intestinalis	-0.0966
Ulva lactuca	-2.1918
Enteromorpha linza	0.3620
Placamium cartilagineum	-0.3916
Palmaria palmata	0.0611
Ceramium rubrum	-0.0212
Saytosiphon lamentaria	-0.1740
Chorda filum	-0.0797
Kelp spp	0.0622
Fucus spp	0.0390
Furcellaria lumbricalis	-0.2908
Disea carnosa	-0.0120
Chthamalus montagui	-0.2079
Pomotoceros triqueter	-0.0886
Umbonula littoralis	0.0860
Botryllus schlosseri	0.0601
Botrylloides leachi	-0.0628
Didenmum spp	-0.2999
Green filamentous	-0.3631
Brown filamentous	4.6337
Red filamentous	0.0365
Kelp spp	0.0304
Bugula falbellata	0.0134
Cladophora rupestris	0.0747

The structural niches available on each of these surface complexities did not alter the community composition found on any of the surface complexities used. The initial settler under this type of disturbance regime was brown filamentous algae, and from the overwhelming percentage of its occurrence in every type of niche available, it seems that it was able to settle and succeed in all types of structural niche (Table 4.12a-d). Cross tabulation statistics confirm this very strong significant relationship ($P < 0.001$), which was present on all surface complexities due to brown filamentous algae.

Table 4.12a – Percentage occurrence of species on each of the structural niches available for settlement on smooth panels in the physical disturbance (P) and hydrodynamic shear (H) experiment where: ● - >70 % ● -61-70% ● -51-60 % ● -41-50 % • -31-40 % • - 21-30 % • - 11-20 % · - 0-10

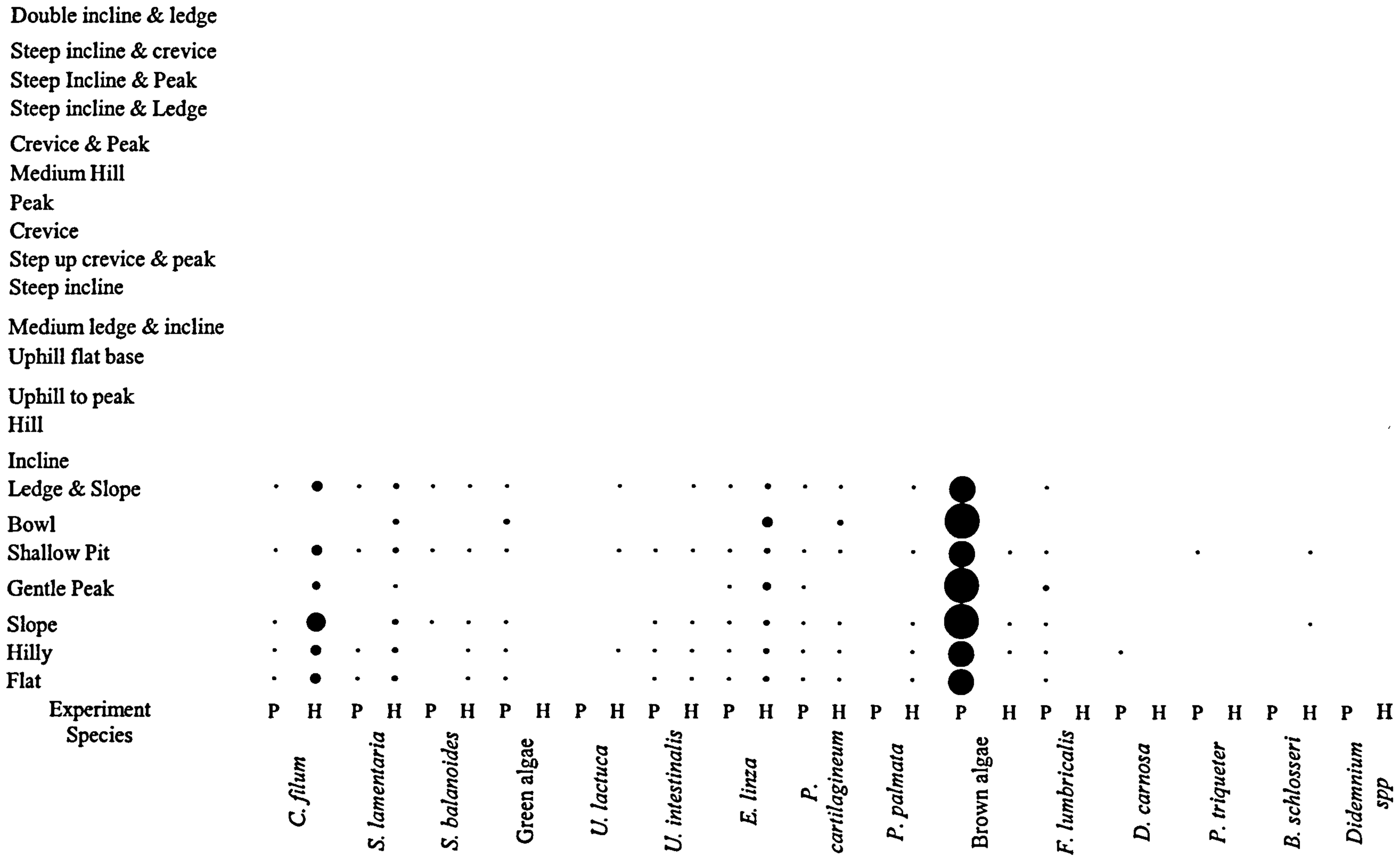


Table 4.12b – Percentage occurrence of species on each of the structural niches available for settlement on R1 panels in the physical disturbance (P) and hydrodynamic shear (H) experiment where: ● ->70 % ● -61-70% ● - 51-60 % ● - 41-50 % • - 31-40 % • - 21-30 % · - 11-20 % · - 0-10 %

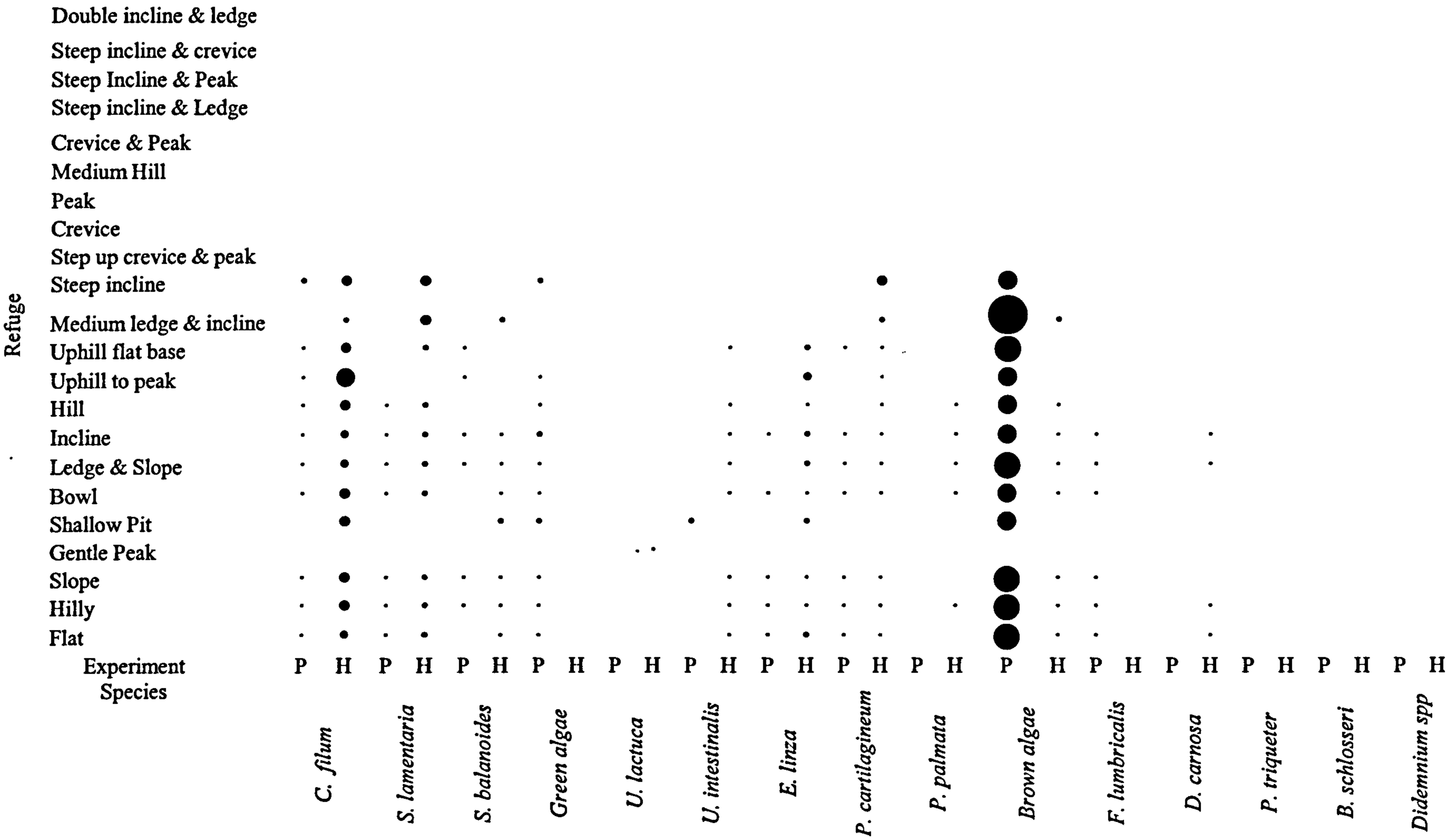


Table 4.12c – Percentage occurrence of species on each of the structural niches available for settlement on R2 panels in the physical disturbance (P) and hydrodynamic shear (H) experiment where: ● ->70 % ● -61-70% ● - 51-60 % ● - 41-50 % • - 31-40 % • - 21-30 % • - 11-20 % · - 0-10 %

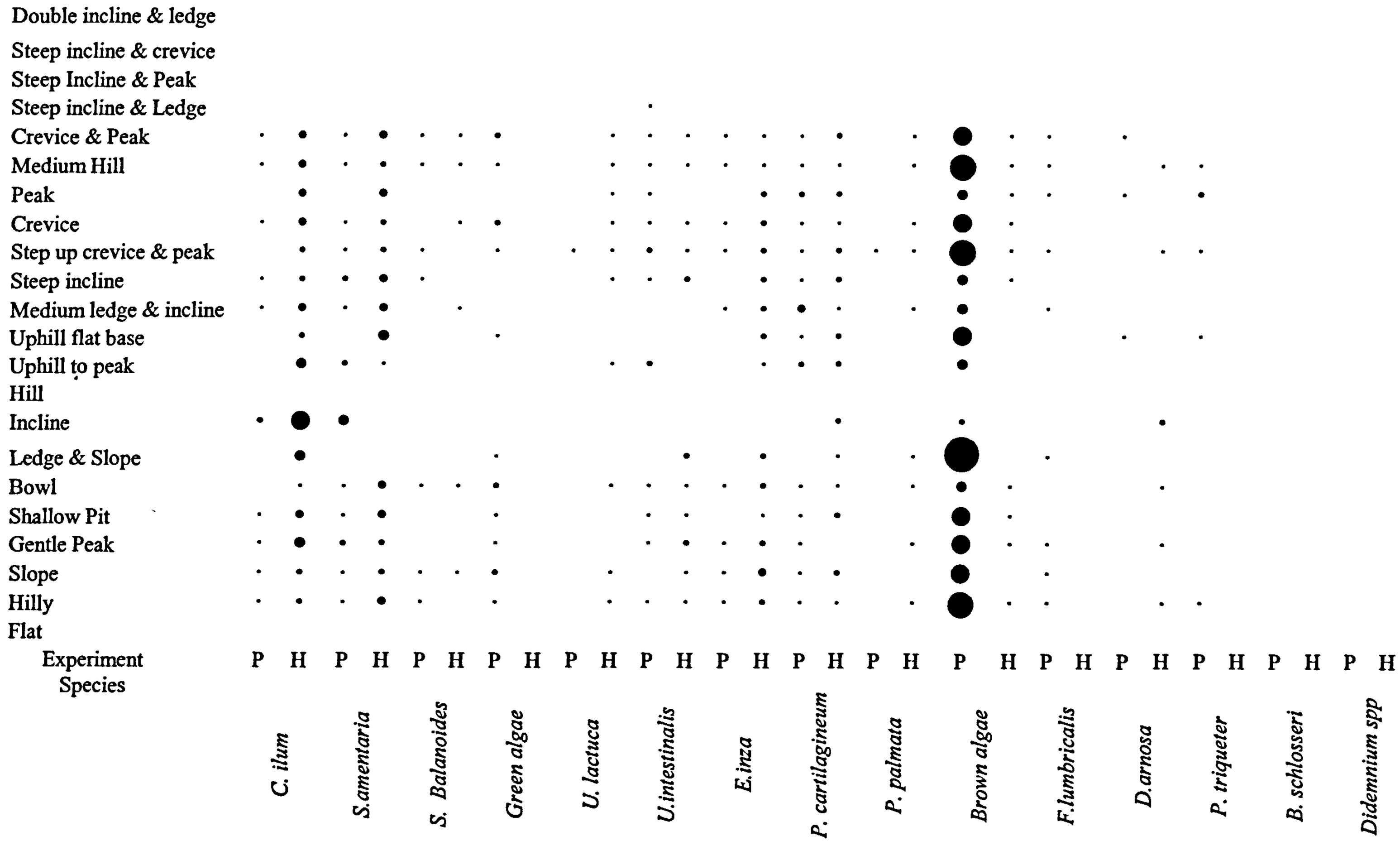
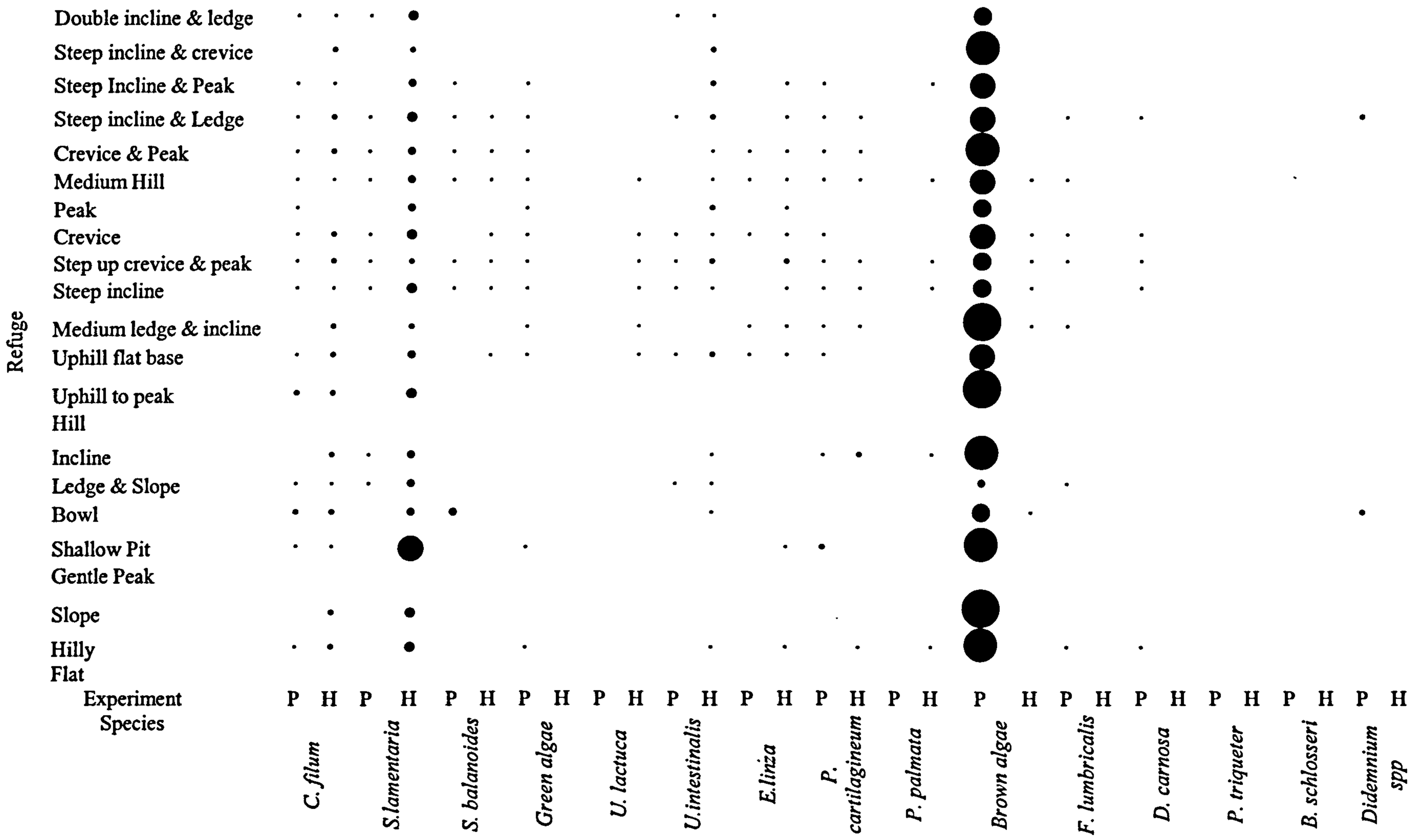


Table 4.12d – Percentage occurrence of species on each of the structural niches available for settlement on R3 panels in the physical disturbance (P) and hydrodynamic shear (H) experiment where: ● ->70 % ● -61-70% ● - 51-60 % ● - 41-50 % • - 31-40 % • - 21-30 % • - 11-20 % · - 0-10 %



4.3.3 – Hydrodynamic shear experiment

Repeated measures ANOVA showed that there were always significant effects of time, on all diversity parameters measured, in the subtidal communities undergoing hydrodynamic shear. There were no significant effects of surface complexity or interactions between surface complexity and time (Table 4.13, Fig. 4.20). Despite this a very clear pattern could be seen in the succession of these communities over time with differences in community composition appearing between levels of surface complexity (Fig 4.21).

Table 4.13 – Repeated measures ANOVA for communities experiencing hydrodynamic shear. Significant values are highlighted in grey where: SS = type III sums of squares, df = degrees of freedom, MS = mean sums of squares, F =F-value, P =probability of significance at α *<0.05.*

Dependant Variable	Source of Variation	Hydrodynamic Shear				
		SS	df	MS	F	P
Shannon index (H')	Time	54.575	8	6.822	116.953	≤0.001
	Time x Surface Complexity	1.755	24	0.073	1.254	0.206
	Surface complexity	0.752	3	0.251	2.218	0.119
Species Richness	Time	1988.108	8	248.513	170.244	≤0.001
	Time x Surface Complexity	32.698	24	1.362	0.933	0.557
	Surface complexity	18.652	3	6.217	2.686	0.076
Evenness	Time	1.026	3.394	0.302	6.670	≤0.001
	Time x Surface Complexity	0.403	10.181	0.040	0.873	0.564
	Surface complexity	0.052	3	0.017	1.012	0.411
Total Abundance	Time	139689.748	3.643	38340.575	191.329	≤0.001
	Time x Surface Complexity	2903.691	10.930	265.658	1.327	0.229
	Surface complexity	883.881	3	294.627	3.123	0.050

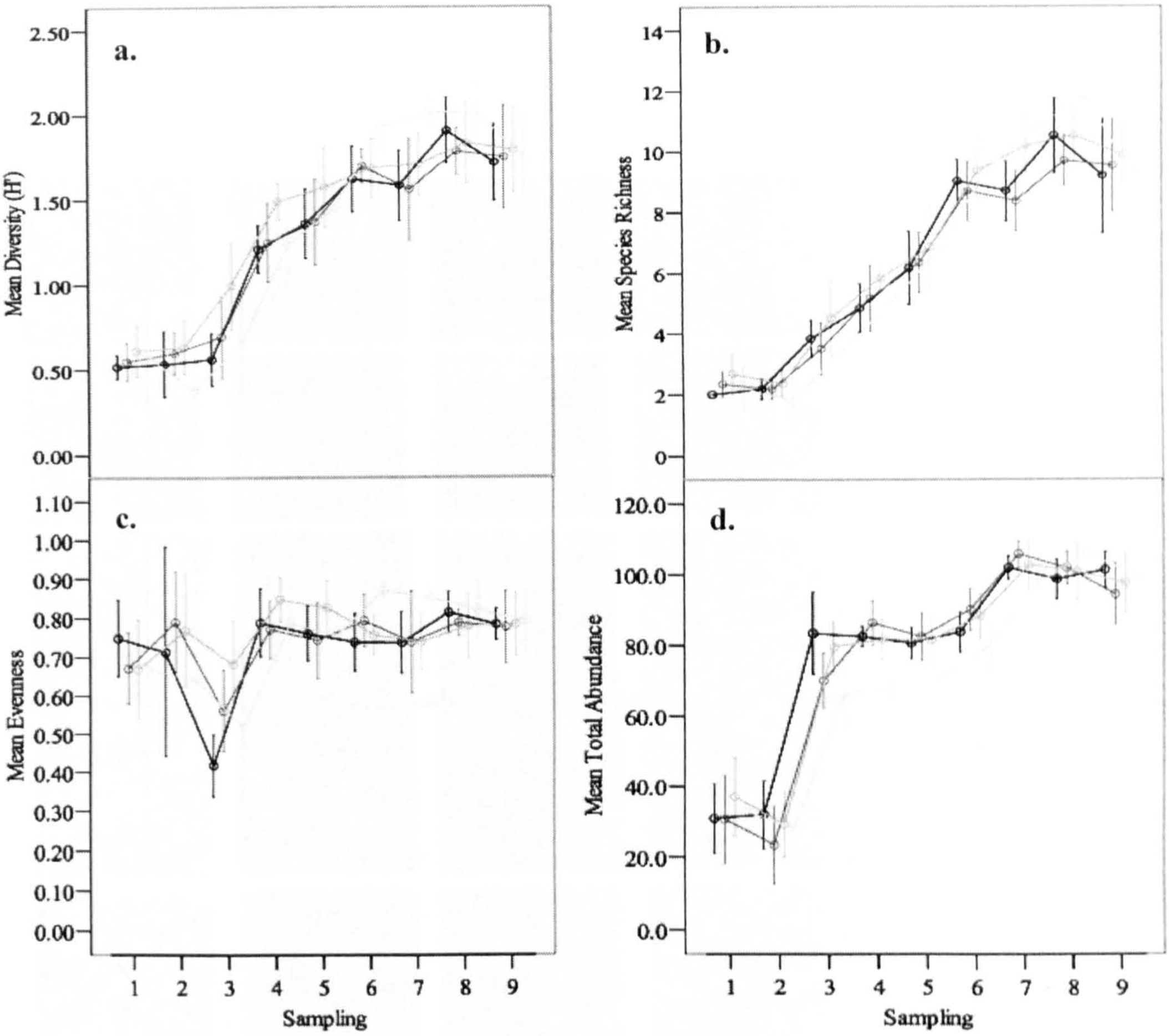


Figure 4.20 – Mean (± SE) a. diversity (H'), b. species richness, c. evenness and d. total abundance for communities subjected to hydrodynamic shear on the different levels of surface complexity: R1 - ——, R2 - ——, R3 - ——, R4 – —— (n = 6 per treatment, per sampling).

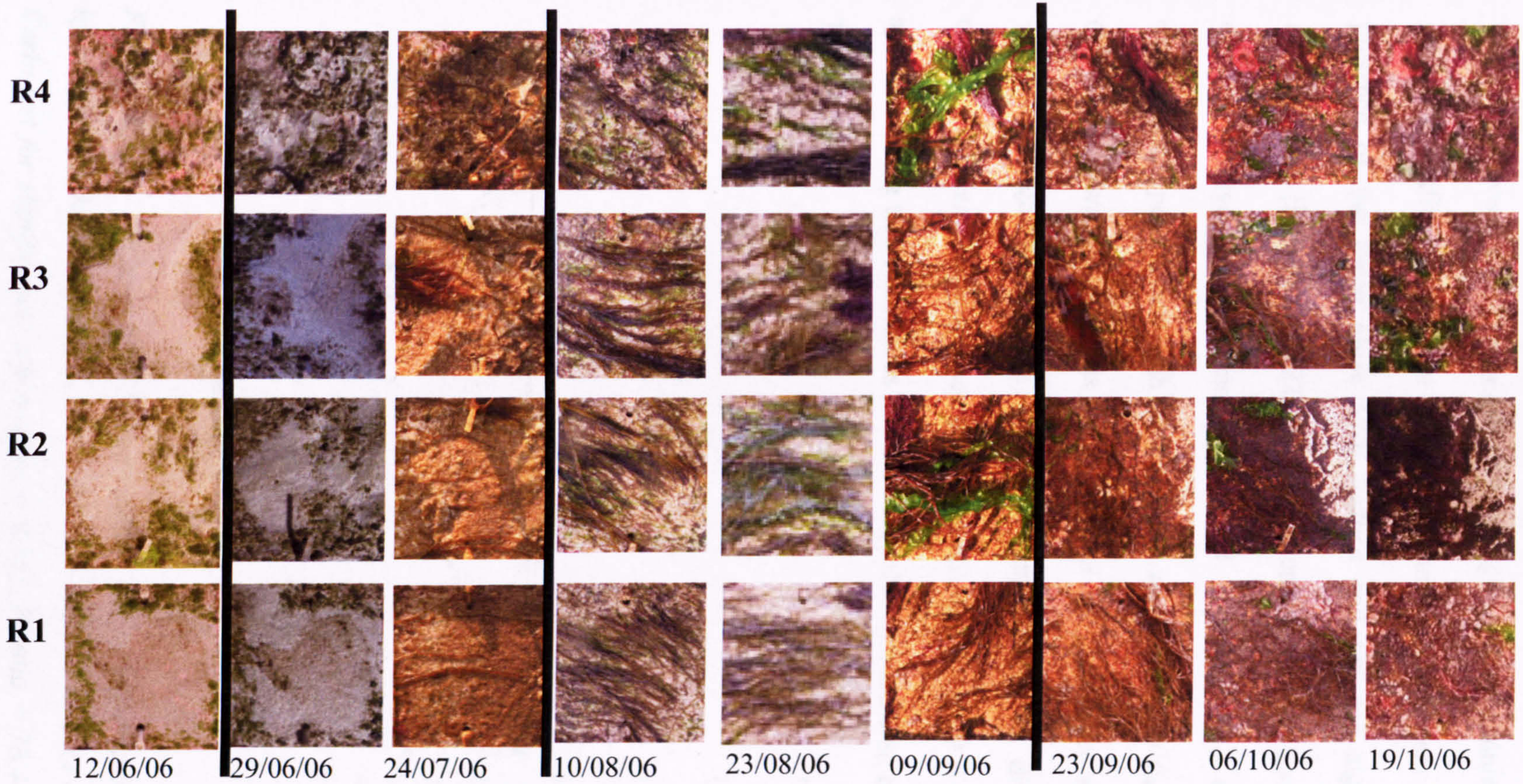


Figure 4.21 - Development of communities experiencing hydrodynamic shear over the nine sampling dates on the four levels of surface complexity: R1, R2, R3, R4, black lines represent disturbance events.

PRC showed that communities on the most complex surfaces (R4) diverge from the less complex surfaces after the fourth sampling date (and the second disturbance event) and remain different throughout the remaining experimental period. The differences seen in community compositions appear to be due to the presence of the green algae *Ulva lactuca* and the red algae *Plocamium cartilagineum* (Fig. 4.21 & 4.22). The two intermediate complexities (R2 & R3) do not diverge greatly from the control surfaces (R1) throughout the experimental period, although at the third sampling date there is a large difference between all surfaces and the control, the effects are not lasting (Fig. 4.22). Although the differences between communities on different surface complexities can clearly by seen they were not significant (P = 0.272) and the species scoring that contributes to the divergences that are seen can be found in Table 4.14.

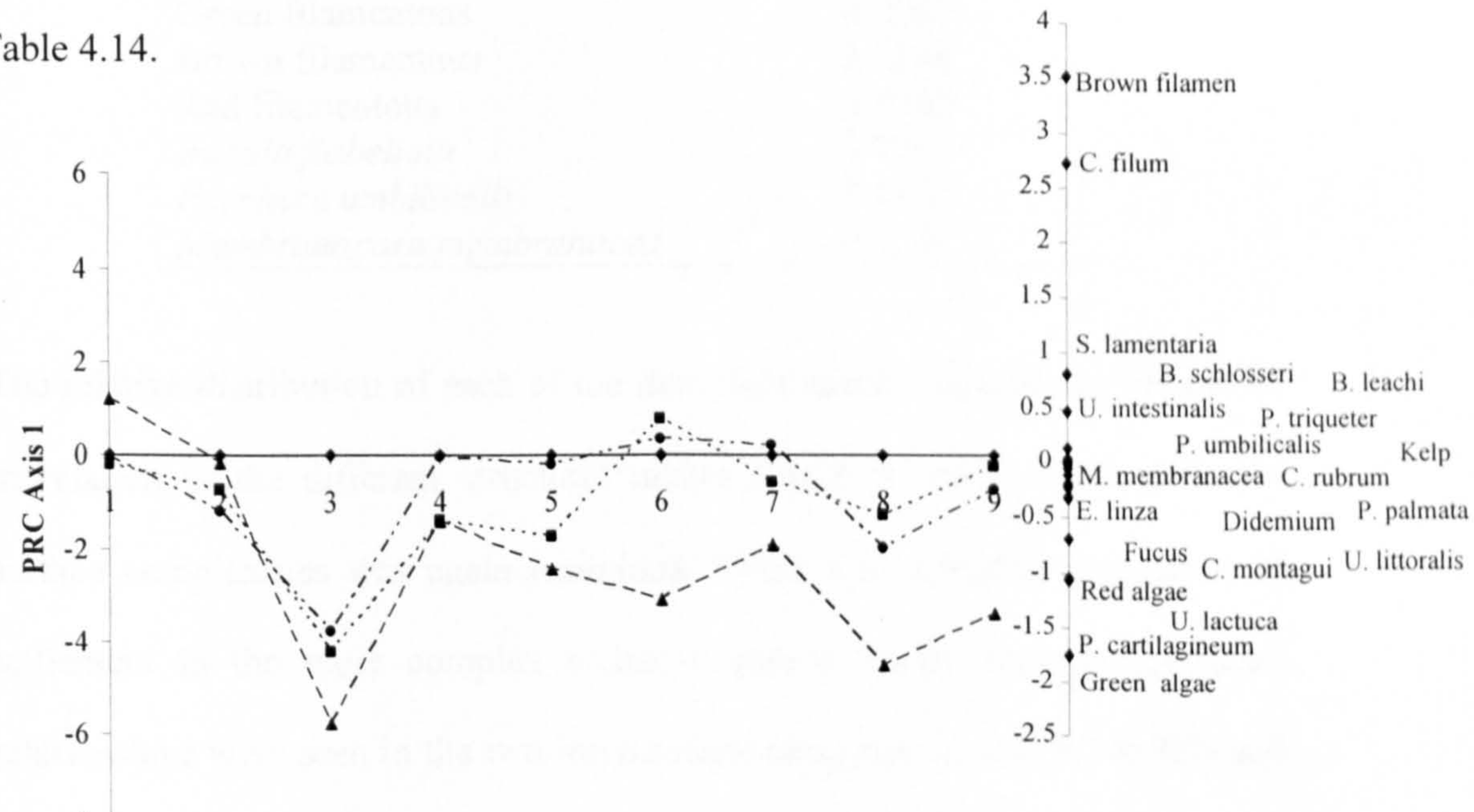


Figure 4.22 - Principal response curve for communities undergoing hydrodynamic shear where: R1 -◆- , R2 --●-- , R3 -·■·- , R4 -·▲·- . Monte Carlo test for significance: eigen-value = 0.253, F ratio = 78.444, P-value = 0.0020.

Table 4.14 - Species scores comprising the principal components analysis for communities undergoing hydrodynamic shear

Species Names	Species Scores
Ulva intestinalis	0.1253
Ulva lactuca	-1.0445
Enteromorpha linza	-0.0348
Placamium cartilagineum	-1.7468
Palmaria palmata	-0.3108
Ceramium rubrum	-0.0338
Saytosiphon lamentaria	0.8240
Chorda filum	2.7410
Kelp spp	-0.2079
Fucus spp	-0.0649
Furcellaria lumbricalis	-0.0299
Disea carnosa	0.0305
Chthamalus montagui	-0.1223
Pomotoceros triqueter	-0.0177
Umbonula littoralis	-0.2123
Botryllus schlosseri	0.4628
Botrylloides leachi	-0.3296
Didenmum spp	-0.6989
Green filamentous	-0.2386
Brown filamentous	3.5298
Red filamentous	-1.0548
Bugula flabellata	0.0064
Porphyra umbilicalis	-0.0033
Membranapora membranacea	0.0066

The relative distribution of each of the dominant species in these communities in relation to the different structural niches found on each of the different surface complexities was again examined. There was a higher proportion of settlement in the more complex niches (Table 4.12a-d). Strong significant relationships were seen in the two intermediate treatment levels (R2 & R3) and they were habitat and species dependent respectively ($P < 0.05$). In surface complexity R2 this could be attributed to a greater occurrence of 'Hilly' and 'Slope' niches, where as on surface complexity R3 there was a greater occurrence of *Chorda filum* in 'Medium hilly' niches than that expected by chance settlement. Relationships on smooth and surface complexity R4 were not

significantly different from that expected by the chance settlement of a species in a particular structural niches.

4.4 – Discussion

The experiments described in this chapter aimed to investigate the effects of small-scale surface complexity within a rocky shore habitat and determine whether species diversity was increased when more complex surfaces were available for settlement. The experiments also aimed to determine whether the structural niches that are provided by the topographical structures within each level of surface complexity promote species diversity in the face of three types of abiotic disturbances common in this type of habitat. As well as discovering if the community compositions are changed with the availability of different structural niches as they provide a refuge against the disturbances. Habitat complexity plays a major role in determining the diversity and species composition of communities on rocky shores (Witman 1985, Denny 2006) and it is only recently that the spatial and temporal scales of this complexity have been recognised as key requirements to understanding the dynamics of ecological systems (Lawrie & McQuaid 2001). Topographically complex areas are thought to provide an increase in niche diversity as well as an increase in the area available for occupation (Johnson et al. 2003), therefore producing a refuge for survival. Such a refuge may provide a relatively safer place to live and should be considered as one of the most important factors governing the distribution and diversity of species on rocky shores (Berryman & Hawkins 2006).

The types of abiotic disturbances that were investigated included exposure in the intertidal zone, and physical disturbance similar to that created by crushing,

and hydrodynamic shear created by wave action in the subtidal zone. All of these types of disturbance are thought to become more prevalent as global climates change. With warmer dryer winters (Harrison et al. 2006) the effects of desiccation stress for intertidal organisms is likely to increase, bringing into question the survival of common rocky shore species that are present today. If these species cannot tolerate this increased stress they may not be able to survive in this type of habitat resulting in increased competition elsewhere, i.e. lower down the shore, and the possibility for the invasion of exotic species that can survive (Harley et al. 2006). Changes in global climate will also bring about more frequent and intense storms, and although benthic species are highly adapted and resilient to this type of disturbance, the effects of an extreme increase in their occurrence is not known. The increase in intensity of these storms will increase wave action and therefore hydrodynamic shear as well as mortality by crushing and impaction (Michener et al. 1997).

The effects of surface complexity on the diversity (H'), species richness, evenness and total abundance of communities was strongly dependent on the type of disturbance that it was being subjected to. Communities in the desiccation experiment that experienced the lowest amounts of exposure were significantly affected by surface complexity, whereas those exposed for longer were not. The more complex a surface was, and therefore the more refuges it provided, the greater the species diversity and total abundance of these less exposed communities. There were also no significant effects of surface complexity on these diversity indices in communities experiencing either the physical disturbances or the hydrodynamic shear.

The low intertidal zone in rocky shore habitats provides an interface between the hardy intertidal species and the less tolerant subtidal species where both are able to co-exist, potentially making it an area of increased diversity (Anthony & Kerswell 2007). However, this not only depends on the type of niches available but also on the competitive abilities of all species present in the community as well as the availability of limiting resources, in this case space. Perhaps an increase in surface complexity provided an increase in the availability of structural niches for this area of overlapping interfaces. These structural niches were not available on the less complex surfaces therefore reducing the potential settlement of certain species that were not able to occupy any space in the presence of stronger competitors or faster growing individuals. It is however surprising that the increase in surface complexity did not have any effect on communities that were exposed for a longer period of time. It would be logical to assume that increased structural niches providing refuges such as crevices, would provide protection not only from predators (Woodin 1978, Menge & Lubchenco 1981, Gillinsky 1984) but also offer desirable resources during times of emersion (Beck 1998, McAbendroth et al. 2005), which would be more attractive to the settlement of a more diverse range of species (Frost et al. 2005, Kostylev et al. 2005). However this is not the case in these communities, there are obviously more factors involved in the consideration of a particular area of substrata to permanent settlement other than just the complexity of the surface, for example the presence of conspecifics may play an important role for barnacles (Connell 1961).

However, diversity indices are not necessarily the most effective way to measure a community's response to a given variable. Diversity indices are commonly used throughout the scientific community as a means to gain an overall picture of the response of ecological communities to a specific set of variables (Magurran 1988). However the nature of calculating these indices relies on combining all of the initial and informative data gathered into one single value, inevitably losing a large portion of the resolution of a particular data set, i.e. species identity is ignored. It is more useful to use the raw data gathered on each of the species to investigate the dynamics of the community, especially when examining the effects of disturbances. The diversity parameters measured before and after a particular disturbance event may therefore appear to show no change in the community: diversity (H'), evenness and species richness all remain the same. However, this does not mean that the dynamics of the community have not changed, upon closer investigation into the composition of the communities, it may be that the disturbance has caused a complete mortality of one species and the free space created has allowed the invasion of a completely different species, potentially one that was not native to the area in the first place. If the resolution of the analysis had not been increased, this community would not have appeared to change, but as a result of the disturbance the entire functioning and stability of this community could now shift in response to this introduced species. This is an extreme example but it highlights the importance of looking a little further into the compositions of communities when examining their responses to disturbances.

In the desiccation experiments community compositions were different from one another the more complex the surface of the panel at both levels of exposure. This was due to the abundances of the red algae *Porphyra umbilicalis* that took advantage of the increased complexity and resources, such as water, that they provided. In the subtidal experiments, those undergoing physical disturbances and hydrodynamic shear, the refuges provided by the more complex surfaces became more important after a series of disturbance events, showing a change in community composition with a reduction in the algal species present and an increase in the invertebrate species present. Clearly showing that although there was no change in the indices measured, that actually the dynamics within the community were changing, a pattern which can clearly be seen by simply looking at the photographs over time for each of the surfaces but which is lost in the very statistics which are used to discern it.

The refuges offered by a range of surface complexities are important for increasing the co-existence of species as well as providing vital areas of shelter against the common abiotic disturbances present in rocky shore environments. Pits and crevices have been shown to offer protection against extreme physical disturbances (Bergeron & Bourget 1986), as well as being the preferential settling site for many types of barnacles (Hills et al. 1999). They are thought to offer cooler, darker and damper areas to live than the peaks associated with them and so offering a refuge against high temperatures and exposure, potentially making them a more desirable place to exist (Bergeron & Bourget 1986). Refuges also offer a buffering against strong water movements as well as channelling a greater proportion of food/nutrients into an area (Denny 2006).

The position of the organisms on each of the levels of surface complexity was dependent upon the type of refuge that was available. There was a greater proportion of species on the more complex surfaces but barnacles seem to prefer to settle in refuges that offer a shallow pit or an incline more than those that offered a peak. This is also seen in some of the algal species within the community and although diversity was always lower higher up the shore the species that were present were always in greater abundance the more complex the refuge was. Initial settlement in the subtidal communities is dominated by the algal species when physical disturbances are imposed, but with increased hydrodynamic shear preventing the settlement of the predominant brown algae, a more diverse community of algae and invertebrates occurs. Subtidal communities experiencing both types of disturbances also have greater species diversity the more complex the surface is and once again the complex refuges do provide protection from the abiotic disturbances tested herein. By quantifying the protection of organisms in a diverse array of structural niches against the common types of disturbances which they are regularly exposed to, it will be possible to assess their ecological role as refuges for these organisms, providing an essential tool for the management of species diversity (Bergey 2005).

As human populations grow the percentage of people living close to the coastline is predicted to increase, resulting in increased urbanization and modification of the landscape in these areas (Bulleri & Chapman 2004). Coastlines are also increasingly threatened by sea level rise and increased occurrence of storms, which result in flooding and erosion at local scales,

prompting the need for more extensive coastal defences (Moschella et al. 2005). The presence of artificial structures such as breakwaters, sea walls and pontoons in marine environments is therefore rapidly growing, resulting in a loss and fragmentation of habitats, which coupled with increasing abiotic disturbances can potentially increase the loss of species from these areas. Understanding the ecological role of these artificial structures is essential to discover whether they differ from natural structures in their diversity and composition in order to plan strategies of conservation and management for the preservation of natural habitats and the species diversity they contain (Bulleri 2005, Bulleri et al. 2005, Moschella et al. 2005). Recent work has shown that although different types of artificial structures produce different compositions of rocky shore species (Bulleri & Chapman 2004) very few appear to adequately mimic the natural communities found close by (Wen et al. 2007). Those that do are suggested to provide a refuge value to the species settling on them that is otherwise not present in the areas where the artificial structures are located (Wen et al. 2007). It is also questionable as to whether artificial structures provide a competitive advantage to invading exotic species over established native species, by offering a place from which they can recruit into the surrounding areas (Tyrell & Byers 2007).

The current work has attempted to quantify the preferential settling sites at the community level of a typical rocky shore assemblage and determine whether these areas offer a refuge against disturbances. By quantifying the value of refuges in this way it may be possible to design artificial surfaces for coastal defence and urbanization, using methods such as the refuge index described in

section 4.2.13. The refuge index described here is however only a first step in quantifying surfaces in this way, much more work is needed to refine this technique and discover whether there is an upper limit to the index where refuges are no longer beneficial but create adverse conditions for species settlement. By creating artificial surfaces in this way it may be possible to promote the settlement of specific native species in direct response to the level of surface complexity and the refuges available within the structures, therefore providing a much-needed tool in an attempt to promote the establishment of 'designer' communities and maximise species diversity.

Chapter Five: Discussion

5.0 – Discussion

The aim of this thesis was to investigate three of the local scale processes that are thought to drive the coexistence of species: abiotic disturbances, productivity and spatial heterogeneity, in temperate benthic subtidal habitats. This was addressed using multifactorial field experiments at three sites on the North East coast of England. The sites used provided a range of conditions from a very sheltered area with limited water exchange (Hartlepool Marina), a less sheltered area with constant water exchange (Sunderland Marina), and an exposed area of natural coastline (Low Newton by the Sea). The studies described within this thesis were designed to:

1. Provide a measure of the resilience of benthic communities to a range of disturbance frequencies and the interaction between these frequencies and different levels of nutrient availabilities.

2. Determine whether an alteration in the temporal variability of a set disturbance regimes affected the species diversity and composition of communities.

3. Establish whether changes in the local scale heterogeneity of surfaces available for settlement by these communities changed the diversity and composition of communities, and provided refuges for specific species against the common abiotic disturbances in this environment: physical crushing disturbance, hydrodynamic shear and desiccation stress.

These studies endeavoured to provide information on the potential responses of communities to the predicted effects of global anthropogenic change, namely the increased occurrence of natural disturbance events, alongside changes in their timing, geographical distribution and severity as predicted through climate change models, coupled with the remaining four principal threats to biodiversity:

- Habitat loss, fragmentation and destruction
- Pollution
- Introduction of exotic species and diseases
- Overexploitation

This thesis has highlighted the importance of abiotic disturbances on species diversity and community compositions in temperate benthic subtidal ecosystems. The abiotic disturbances studied herein are essential to maintain the dynamics of the communities investigated, resetting succession, preventing dominance by a single species and allowing co-existence. Disturbances effectively opened up free space, a key limiting resource in this environment, resulting in a mosaic of patches of communities at different successional stages.

5.1 – Disturbances

Connell (1978) introduced a non-equilibrium view of ecology, where communities of organisms are continually changing, rarely reaching a stable climatic state. Connell proposed a number of concepts to explain this viewpoint,

the most famous and widely used of which is the intermediate disturbance hypothesis (IDH: Connell 1978). There have been a number of studies on the IDH and it is regularly cited as the reason for increased diversity in certain areas (Dial & Roughgarden 1998, Huxham et al. 2000, Roxburgh et al. 2004). Despite this, empirical support for the hypothesis is not as strong as its use suggests (Mackey & Currie 2001). The frequency of disturbance regimes that were examined in Chapter 2 did not support the IDH as proposed by Connell (1978) in the communities investigated, nor did they support the interaction between different availabilities of nutrients as proposed by Kondoh (2001) and Huston (1979).

Benthic communities in temperate regions have strong seasonal patterns of recruitment and growth suggesting that the timing of disturbance events upon these communities could have important implications for their resilience and survival. If as predicted, disturbance events become more variable with global change, they will result in a clustering of severe events; in the long intervals associated between clustering, competitive species will dominate the community but as disturbance events begin and continue the competitive species would disappear and the community may not then have enough resilience to recover. The clustered events may coincide with the growth rates of certain species inadvertently favouring rarer or introduced species in the community. Temporal disturbance events could begin to coincide with periods of recruitment enabling the settlement of certain species whilst preventing that of others and the area-margin ratio of space created by the increased events could

influence whether recovery is from lateral in-growth or settlement of propagules.

Benthic communities on rocky shores live in characteristically heterogeneous habitats that comprise a number of levels of complexity. The heterogeneity of the surfaces upon which they live is another very important mechanism thought to drive co-existence. However, the importance of this heterogeneity as a mechanism to provide refuges against common types of disturbances in rocky shores has rarely been studied. Experiments supported the view that more complex habitats increased species diversity, but also suggested that the presence of specific types of refuges facilitated the settlement of certain species as well as protecting them from different types of disturbances.

5.2 – Threats to biodiversity

Ecologists, under the premise of anthropogenic global change, come under increasing pressure to understand, explain and predict the responses of nature to increased pressure (Chapin et al. 2000, Straton 2006). The Earth is currently experiencing an unprecedented extinction crisis which is facilitated by five principal threats, including climate change, which have been previously outlined (Wilson 1988, Soule 1991).

These threats are often investigated independently of one another (Acosta 1999, de Boer & Prins 2002, Guidetti et al. 2003, Piazzi & Cinelli 2003, Harley et al. 2006, Fischer & Lindenmayer 2007) with each resulting in severe impacts on

ecological systems. The overall picture however is not that simple. The five principal threats outlined above all interact with one another, creating positive feedback cycles that work to speed up the loss of biodiversity that is being observed (Chapter 1; Fig. 1.1). This model however is not independent of the mechanisms (disturbance, productivity, spatial heterogeneity) that are thought to control species diversity, each of the mechanisms, for example a disturbance, will link into this model having one of two effects depending on the resilience of the ecosystem in question. The natural community, which is already stressed by one or more of the principal threats, will either recover from a disturbance event or it will lose a portion of its ecosystem functioning, facilitating the principal threat (Fig. 5.1).

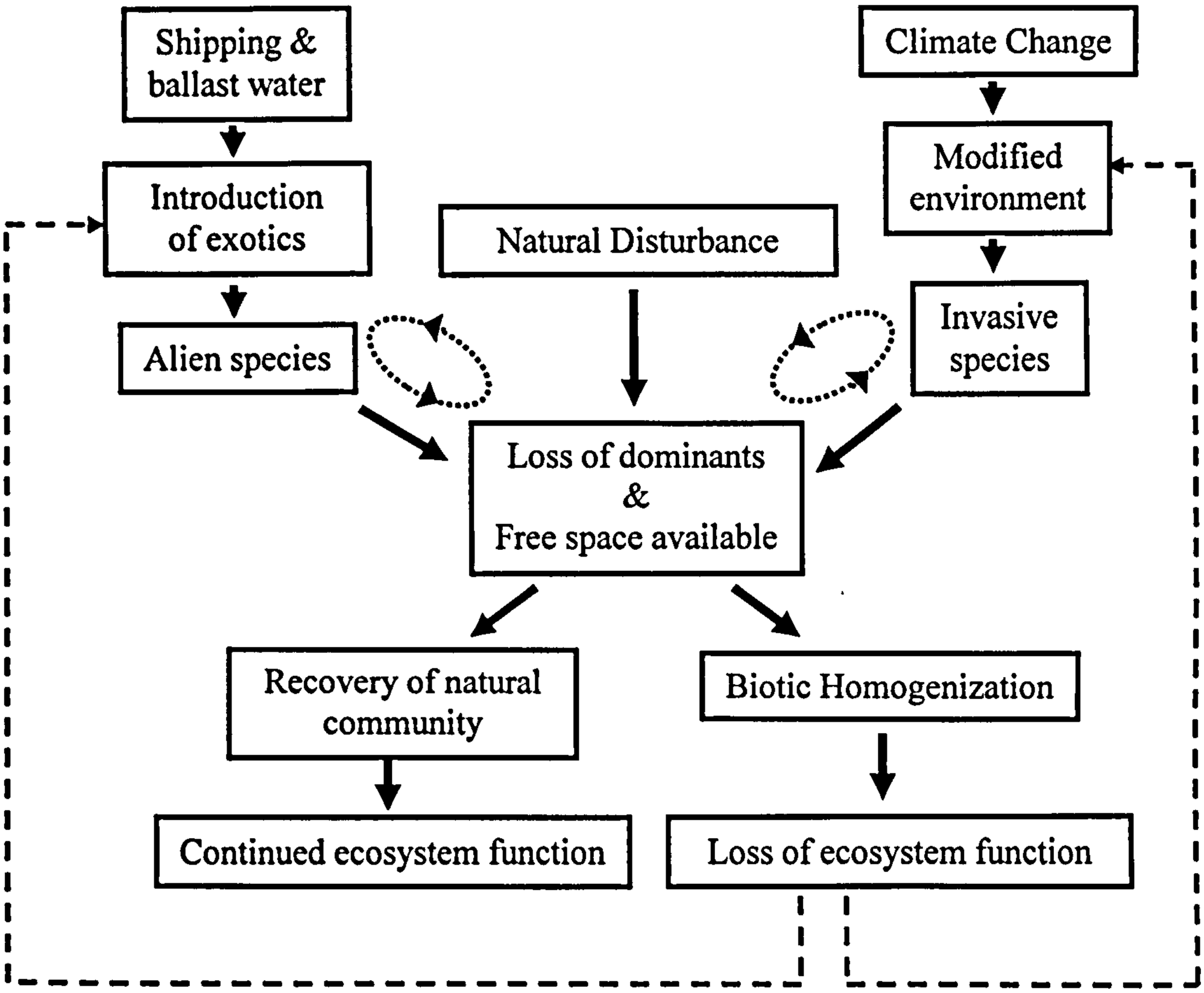


Figure 5.1 – The interactions between two of the principal threats to the loss of biodiversity, climate change and the introduction of exotic species, and the proposed outcome of their interaction with natural disturbances on rocky shores, where ⟶ represent direct effects, – – ▸ represent facilitating effects and ⟲ represent positive feedback cycles.

Disturbances in temperate rocky communities are natural and common as well as essential to act as a tool to reset succession and allow the co-existence of species (Dayton 1971). Using the example from the model, if a natural disturbance coincided with the arrival of an invasive or exotic species, either

from shipping or as a result of the modification of cooler environments from atmospheric warming by climate change, the natural disturbance could facilitate the establishment of the non-native species in an area where it had never previously been observed. The natural community may however be very resilient, out-competing the invasive species reducing its potential for survival. But it may not; the introduced species may be a superior coloniser, able to take full advantage of the newly opened up space and freed resources created by the disturbance, eventually allowing it to out-compete surviving native species and dominate the ecosystem.

The implications of this to the continued functioning of the ecosystem are unknown and potentially severe. High levels of biodiversity within ecosystems are thought to promote resilience and increase functioning, sustaining vital ecosystem services, such as fresh air and clean water, which are essential to the continued survival of the biosphere (Costanza et al. 1997). The example above is a simplified one which takes into account only one of the proposed outcomes of one of the principal threats to biodiversity, there are many more, each facilitating the others (See Chapter 1).

Natural systems are multi-dimensional with numerous processes and interactions simultaneously occurring to produce a community of species. The experiments conducted as a part of this thesis add support to the non-equilibrium concept of species diversity where disturbances are important mechanisms for the co-existence of species. Despite this, the simple conceptual models that were tested as a part of the experiments were not supported, adding

further support to the idea that many processes are simultaneously interacting to produce a community of species. Simple conceptual models therefore need to be extended to take into account more mechanisms in order to succeed in predicting patterns of diversity. It is obvious from this work that where one model may adequately explain and predict biodiversity in one system it may not be immediately applied to another system. In order to achieve the goal of sustaining biodiversity, predictions must be system specific. The work carried out herein was also field based and this is essential to gain an understanding of what is actually happening under natural conditions. Although multifactorial experiments in the field have their limitations and can never incorporate all of the factors involved, they are necessary to gain an understanding of what is important for the survival of species.

Another important finding from the work carried out here was the identification of particular types of refuges, for species, against disturbances, in complex habitats. If, as predicted, extreme disturbance events become more frequent and severe, refuges could become an important step in the conservation of communities. The identification of species specific refuges could also be important for managing ecosystems. As urbanisation of the world's coastline increases through the building of breakwaters, marinas and flood defences, the natural habitat associated with the coastline, such as rocky shores, is lost (Bulleri & Chapman 2004, Moschella et al. 2005). It has already been suggested that the species living on the artificial structures are different to those living in natural environments (Wen et al. 2007) the effects of these species replacements on ecosystem functioning and the services they provide is largely unknown.

5.3 - Further Work

Although the conclusion that disturbances are important structuring mechanisms in benthic communities was supported at a number of sites globally, this study would benefit from further research encompassing a range of seasons in each area of study, as well as an alteration of the disturbance frequencies specifically modified from the previous set of frequencies and based on the area of study. With more work it could also be possible to identify the type of refuge that a particular species prefers to settle in, therefore allowing the creation of an artificial structure that promotes the settlement of specific species and therefore communities that are comparable to those naturally occurring in the area of interest.

5.4 - Conclusions

The threats to species diversity outlined in this chapter are occurring and it is no longer possible to ignore the predicted consequences of these threats. Severe storms and flooding are already much more frequent, our natural defences to which have been largely destroyed. In order to slow down, stop or reverse the effects of the ecological footprint of our own species, it is essential to understand the dynamics of ecological systems so that they can be effectively managed and conserved, if only to maintain the services that are essential our own survival. An understanding of the key elements governing ecosystems must firstly be gained so that the processes of disturbances, productivity and spatial

heterogeneity may be unravelled under the template of spatial and temporal variability. In order to comprehend how these forces interact it has always been essential to consider them individually, but simple models do not tell the whole story and it is now important to consider them in a larger framework. There will always be a trade-off between realism and adequate statistical power but by continuing to conduct multifactorial experiments in the field over a variety of spatial and temporal scales it will be possible to build a more detailed picture of what is important to the continued survival of many species, hopefully in time to conserve what is left of the unique planet in which we struggle to survive.

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